SYSTEMATICS AND PALAEOBIOLOGY OF

HAAST'S EAGLE (*Harpagornis moorei* Haast, 1872)

(Aves: Accipitridae)

A thesis

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Richard N Holdaway

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To my Mother

Olive Grace (Grace) Holdaway

1913-1977

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Abstract

A phylogenetic analysis of the family Accipitridae was based on 188 osteological characters for 44 living genera, plus Haast's Eagle (*Harpagornis moorei* Haast, 1872), a large fossil species from the New Zealand Quaternary. Haast's Eagle is sister group to the *Aquila* eagles, which are themselves close to forest eagles of the genus *Spizaetus*. Most major groups recognised before were present, but some new groupings were revealed. Haast's Eagle is represented by copious material from over 40 sites, with more than 60 individuals. One 99% intact skeleton is known. A second nominal species (*Harpagornis assimilis* Haast, 1874) is a junior synonym of *H. moorei*, and possibly represents the smaller male. The eagle's distribution did not match major environmental patterns, but appears to have been associated with a group of species of moas, Dinornithiformes. The eagle's distribution apparently changed with the climatic amelioration at the end of the Otiran glaciation, when it apparently retreated from northern and western areas as these became clothed in dense, wet forest. In the Holocene, it was most abundant in the east and south of the South Island, where there was a mosaic vegetation pattern of drier forest and shrublands. It was rare, or absent from inland and northern North Island districts during the Holocene. Sites in caves represent pit traps that caught eagles that entered to take live prey, probably large ground birds. Swamps may have trapped eagles that were attacking trapped moas and other birds, but the evidence is equivocal and specimens may represent natural attrition from a population. However, claw marks on 10% of moa pelves from birds in the 80-100 kg weight range in Canterbury Museum collections provide strong support for the predation hypothesis. The distribution of the eagle and its major potential prey species also support an hypothesis of an active predator rather than an obligate carrion eater. Ecomorphological analysis also supports the eagle's role as being a predator. Various multivariate statistical procedures consistently result in Haast's Eagle clustering with large forest eagles that use flapping flight, rather than with gliding eagles or vultures. This does not support the carrion feeder hypothesis. The eagle's wing proportions also suggest that it flapped rather than glided. There was some support for the two sexes having different flight patterns, and possibly different

preferred prey. Haast's Eagle was the major predator in a mammal-free environment. Although phylogenetically an aquilin eagle, Haast's eagle had evolved into the largest, seemingly most powerful, forest and forest margin bird of prey known. The mosaic of features in this species illustrates the extreme plasticity, within narrow functional/historical limits, that characterises the Accipitridae.

1. GENERAL INTRODUCTION

A recent renaissance in interest in fossil avifaunas from islands has been stimulated largely by work in Hawaii (e.g., Olson & James 1982, 1984), the South Pacific (Steadman 1985, 1986a, 1986b, 1988), and the West Indies (Olson & Hilgartner 1982). These and other studies have demonstrated the diversity of island avifaunas before human colonisation, and their extreme vulnerability to external influences, including the processes associated with colonisation (Olson & James 1984; Cassels 1984; Steadman 1986). Recognition of the amount of diversity lost has in turn stimulated interest in the structure and palaeoecology of the fossil avifaunas, in an attempt to understand why the systems were so vulnerable. It has become apparent that existing theories of island biogeography and ecology, which often rely heavily on data for island birds, have been based on incomplete, and often heavily biased, samples (Olson 1989; Olson & Hilgartner 1982; Olson & James 1982, 1984).

Renewed interest in the Quaternary fossil vertebrates of New Zealand is shown by increasing numbers of papers on problems of taxonomy, systematics, palaeoecology, and the co-evolution of animals and plants. Recent articles include: Atkinson & Greenwood (1989); Greenwood & Atkinson (1977); Holdaway (1989, 1990 [bound as part of Chapter 4]); Millener (1980, 1981, 1982, 1988, 1989); Worthy (1987a, 1987b, 1987c, 1988a, 1988b, 1990); Worthy & Mildenhall (1989). Progress in this area has relied heavily on radiocarbon dating (Anderson 1990; Worthy 1988b; Worthy & Mildenhall 1989), and a better knowledge of former climates and vegetation patterns based on palynological, glaciological, and oxygen isotope studies (e.g., Burrows 1979, 1982; Burrows & Greenland 1989; Mabin 1983; McGlone 1983a, 1983b, 1988, 1989). There are now sufficient data to support provisional assessments of the major habitats of vertebrate faunas in New Zealand during the late Pleistocene and Holocene (McGlone 1989), the changes brought about by climatic oscillations over the past 30,000 years, and the dramatic changes resulting from colonisation by man within the past 1000 years (Anderson 1983, 1984, 1990; Cassels 1984; Holdaway 1989, 1990; McGlone 1983b, 1989).

In addition, a recent upsurge in interest in systematics, stemming initially from Hennig's seminal work in phylogenetic systematics (Hennig 1966), has resulted in new, rigorous methodologies, which are now being applied to birds of the New Zealand region (Livezey 1986; Siegel-Causey 1988).

Within the developing systematic and ecological framework, it is therefore possible to infer the palaeoecology of individual species with more confidence now than in the past. The ability to assign plausible ecologies to many species has been seen as a key to understanding whole ecosystems and their susceptibility to change (Zimmerman & Bierregaard 1986).

1.1 Raptors

Some of the most important indicators of stress in extant ecosystems are raptorial birds, because being at the peak of the Eltonian pyramid they are especially sensitive to environmental changes. Fortunately, diurnal birds of prey are often conspicuous components of fossil avifaunas from Quaternary deposits (Howard 1932; Steadman & Martin 1984), especially those from geographical or ecological islands (Arredondo 1976; Ballmann 1969, 1973).

Island faunas from Cuba (Arredondo 1976), and the Bahamas (Olson & Hilgartner 1982) contained very large raptors that were apparently the largest predators in their particular ecosystem. Both accepted species of Accipitridae named from New Zealand were exceptionally large. Haast's Eagle (*Harpagornis moorei* Haast, 1872) was larger than the living Harpy Eagle (*Harpia harpyja*) of South and Central America, and is the subject of this thesis. The other accipitrid (*Circus eylesi* Scarlett, 1953) was a huge harrier, more than twice the weight of living species of harrier (Holdaway, unpublished data; all observations not supported by references are my own unpublished work and are part of this thesis).

The former presence of a large eagle in New Zealand aroused considerable interest amongst ornithologists at the time of its discovery in the 1870s. The size of the bird, and its association with moas in swamp deposits led to speculations about its habits and rôle in pre-human ecosystems. Forbes (1892) considered the eagle to be a carrion-feeder, depending on dead moas for food -

a vulture. Conversely, Owen (1879) took the view that it actively preyed on the large flightless birds that dominated the pre-human avifauna. The first view has gained most popularity in the popular literature, although little new analysis has been published since the late 19th Century (Hamilton 1893, 1894). The perception of Haast's Eagle as a scavenger, and thus an animal which cannot control, or exert any evolutionary pressure on, a prey population, has led to the eagle's importance in the palaeofauna being underestimated. Studies of moas (Dinornithiformes) dominate the literature of New Zealand fossil birds. The possibility that predator-prey relationships may have been important for moa population biology or evolution has rarely been considered. Indeed, even recent papers state that moas evolved in the absence of predators (e.g., Alexander 1989).

1.2 Systematics and palaeoecology

Two other features of Haast's Eagle have also occasioned comment, but little analysis. First is the relationships of the eagle within the family Accipitridae, an understanding of which has been hampered by a lack of consensus on the systematics of the Accipitriformes and the Accipitridae in particular. Haast (1872, 1874), Owen (1879), Shufeldt (1896), and Oliver (1930, 1945, 1955) suggested various relationships within the family Accipitridae, which presently is considered to contain about 60 genera and 220 species (Brown & Amadon 1968; Stresemann & Amadon 1979).

Slow progress in understanding the relationships within the Accipitridae has been exacerbated both by a lack of comparative material, and by the emphasis placed on external morphological characters by recent systematists (Amadon 1953, 1964, 1977, 1982a, 1982b; Brown & Amadon 1968; Stresemann & Amadon 1979). Difficulty in relating external and internal morphological evidence (Jollie 1976, 1977a, 1977b, 1977c) has been a major barrier to developing an understanding of the relationships among fossil accipitrids in general (Olson 1985).

The second subject of debate has been the preferred habitat of the eagle. Early workers had little information on which to base palaeoenvironmental

reconstructions, and sometimes overlooked evidence revealed in their excavations. It was usually assumed that the vegetation encountered by European settlers in the 19th Century was original (e.g., Cockayne 1928), and that the Polynesians had had little effect on it (Holloway 1954). Therefore it was assumed that the extensive grasslands on the plains and downlands east of the central ranges, and the wet West Coast forests, were the habitats within which the newly discovered living and fossil faunas had always lived.

The eagle was first perceived as a huge harrier, which had followed flocks of moas across the grasslands (Haast 1872). Although it is now well established that the pre-human vegetation of New Zealand, even in dry eastern areas, was forest or shrubland (McGlone 1988, 1989), the concept of Haast's Eagle as a carrion-eater dependent on moas is still strong (McCulloch 1991).

1.3 Background to this study

In 1975, Mr D H Brathwaite presented radical new views on both the relationships and the habits of Haast's Eagle at a Summer School of Ornithology run by the Ornithological Society of New Zealand. His views took into account the new knowledge on the vegetation, and were developed from basic assumptions on habitat and on the aerodynamic problems that would have been encountered by a heavy bird. Brathwaite's new hypotheses maintained that *Harpagornis moorei* was a forest eagle related to tropical hawk eagles of the genus *Spizaetus*. He suggested that, like these birds, *Harpagornis moorei* had the short broad wings and long tail which are characteristic of a forest raptor, and that it could fly well and was an active predator.

As noted above, these views were contrary to the prevailing views (e.g., Duff 1949; Trotter & McCulloch 1984; McCulloch 1982) and they have not been widely accepted (e.g., McCulloch 1991; Stevens 1990). However, they provided the impetus for the present work, and I am immensely grateful to Don Brathwaite for freely sharing his ideas, and for long, stimulating discussions on all aspects of New Zealand's extinct avifauna, and particularly the eagle.

The aims of my study were to test the Brathwaite hypotheses, using the large amount of well-preserved material of the eagle now available, the

taphonomy and mode of deposition of the remains, and the comparative material of other raptors available in major institutions in the USA and United Kingdom. The questions asked can be summarised as: what were the relationships of Haast's Eagle; where and how did it live; and how did it fly?

1.4 Relationships within the Accipitridae

The question of relationships necessitated a revision of the family Accipitridae, based on osteological features, so that the relationships of the fossil taxon could be assessed. A preliminary phylogeny of the Accipitridae based on a cladistic analysis of such features is presented in Chapter 1.

The systematics of the Accipitridae have been controversial for more than a century (Gadow 1893; Friedmann 1950; Brown & Amadon 1968; Stresemann & Amadon 1979; Jollie 1976, 1977a, 1977b, 1977c; Sibley & Ahlquist 1972; Suschkin 1899). The most recent comprehensive treatment (Jollie 1976, 1977a, 1977b, 1977c) did little to resolve the confusion. As my revision was undertaken as an attempt to resolve the relationships of a fossil taxon within a living family, it was fortunate that the material available was complete enough for *Harpagornis moorei* to be treated as a living taxon. This removed one of the problems now recognised with systematic work, that of fitting fossil taxa into a classification based on living taxa (Wiley 1981; Patterson 1988).

Previous efforts at bringing order to the Accipitridae have been hampered by the high diversity of taxa included, and by the complexity of the variation in their structure, both convergent and parallel evolution being recognised as having occurred within the group. I used the most powerful available technique consistent with the data set, that of computer-assisted phylogenetic analysis. This approach had the virtue of being able to cope with the large number of taxa involved, and the large number of features that this number of taxa necessitated my using in the analysis. Optimally at least a 3:1 feature:taxon ratio should be used (Wiley 1981), and this ratio was exceeded in this study.

The data set included nearly 200 multi-state features from most of the major elements of the skeleton for individuals of one or two representative species from 56 genera. This was as comprehensive a coverage as possible within

the limited time available. In addition, many genera are poorly represented in museum skeleton collections (89% of genera represented, and 69% of species with at least one specimen, Zusi *et al.* (1982)), some are represented by a few bones only of the skeleton, and several (such as *Eutriorchis*) are not available at all. Because of the restrictions on intrageneric samples, the study was conceived as purely a preliminary survey and in no way a definitive work.

Some osteological features had been described for a range of taxa, but most were derived *de novo* from an inspection of each bone from as full a range of taxa as possible. As such, the study also represents a survey of features of possible phylogenetic significance within the group.

The opportunity was also taken to assess the osteological similarity between the secretarybird (*Sagittarius serpentarius*) and the osprey (*Pandion haliaetus*), and the accipitrids, with which these two species have been allied at levels from suborder to subfamily (Friedmann 1950; Brown & Amadon 1968; Sibley & Ahlquist 1972).

After the problem of relationships was resolved, the opportunity was taken to redescribe and illustrate the taxon using the much more extensive material now available, and with reference to the type material held at Canterbury Museum. An almost complete associated skeleton recovered from Mount Owen southwest of Nelson was used as the basis for description after it was established as conspecific with the lectotype femur.

1.5 The status of *Harpagornis assimilis* Haast, 1874

Before redescribing the taxon, the status of the second nominal taxon described by Haast - *Harpagornis assimilis* Haast, 1874 - had to be assessed. When naming the second species, Haast had suggested that *H. assimilis* was the smaller male of *Harpagornis moorei*, and other authors had synonymised it with *H. moorei* in lists. Oliver (1955) included both taxa, but no formal decision based on an examination of the material had been published.

Therefore, a morphometric analysis was made of all material available, to test the original discriminating feature, which was an apparent difference in size. The synonymy was confirmed (Holdaway 1990, Chapter 2A here), and the

femur from the type series (CM AV5104pt) was designated as lectotype. All material previously referred to *Harpagornis assimilis* is taken here to represent *H. moorei*.

1.6 Taphonomy

Answering the questions about where and how the eagle lived involved first an assessment and analysis of the distribution of the sites where eagle remains had been found and those where it had not. This analysis considered the type of site, its age and any stratigraphy, the inferred depositional environment, and mode of exposure, and any other aspects of the site and its fossil fauna considered relevant. Reconstructing the living community represented and sampled by a fossil sample is an ultimate object of the field of taphonomy (Behrensmeyer & Kidwell 1985; Holtzman 1979), and includes analysis of the processes associated with the death, decay, disintegration, incorporation in sediments, diagenetic changes during and after burial, and exposure of the remains of organisms as a fossil assemblage. Ideally, these processes must be traced in reverse, with allowance being made for biases introduced at each stage, before a picture of the biocoenosis can be developed (Holtzman 1979).

1.7 The pre-human avifauna

The remains of Haast's Eagle have nearly always been found in association with those of other birds, both living and extinct. Enough is known of the ecology of the living species to allow their presence in a deposit to be used as indicators of past local environments (Baird 1989). A broader picture may be obtained from analysing the overall co-occurrence of species in fossil sites. These two approaches are used in Chapter 4 to build a picture of the bird communities in pre-human New Zealand. Patterns in the association of Haast's Eagle with other species of bird could shed light on its habitat, diet, and any constraints these may have placed on its distribution.

1.8 Ecomorphology

An animal interacts with its environment, and an analysis of its structure and function is essential to an understanding of its ecology. As a member of the Accipitridae, Haast's Eagle had obvious adaptations to a carnivorous diet. Within the Accipitridae, killers and carrion eaters have different flight modes related to energy demands and the distribution of food, although most species are opportunistic and will take living or dead prey as it is available (Brown & Amadon 1968). Carrion eaters usually soar (Pennycuick 1972) and species which kill vertebrates often hunt from perches and chase their prey in short, rapid flights (Brown & Amadon 1968).

The morphometrics of Haast's Eagle were analysed in relation to its predatory potential, a concept introduced by Voous (1969) in a study of the diverse raptor assemblage of Surinam. The hypothesis that Haast's Eagle was a poor flier, and was perhaps evolving towards flightlessness (Duff 1949), was tested by comparing the bird's morphometrics with those of other large raptors whose flight styles and general ecology are known.

The poor flight hypothesis originated with Haast's (1874) observation, repeated by Owen (1879), that the ulna was *relatively* short in comparison with that of other accipitrids, such the Wedge-tailed Eagle (*Aquila audax*) and the Australasian Harrier (*Circus approximans*), both of which habitually glide or soar. With time, the 'relatively' was forgotten, and the ulna was described as simply 'short' (Oliver 1955), a condition, which if true has obvious implications for the bird's flying ability. In conjunction with the long and thick leg bones, the apparently short ulna has been interpreted as indicating a predominantly terrestrial mode of life (Millener 1984). However, none of the speculations concerning wing reduction and leg hypertrophy was supported by references to specimens, or by new comparisons with a wide range of other taxa.

This thesis has developed as a broad survey of a range of diverse problems associated with the palaeoecology of one extinct species of large raptor. The systematic analysis, although purely preliminary and based on a limited sample, has indicated some promising avenues for further study, particularly for further work on a possible close phylogenetic relationship

between the aquiline (Golden Eagle-type) and spizaetine (Ornate Hawk Eagle-type) eagles. These two groups differ widely in their typical habitats and feeding ecology, but appear to be sister groups. From the perspective that several factors, including phylogeny, functional constraints, and historical chance contribute to the present structure and ecology of a group or species (Seilacher 1979), this can be seen as an indication that, contra Mayr (1989), overall similarity is not necessarily a good indicator of relationship.

2. REVIEW OF PUBLISHED INFORMATION AND IDEAS ON HAAST'S EAGLE (*HARPAGORNIS MOOREI*)

This review of published information and ideas on Haast's Eagle is provided to enable the development of perceptions of the bird to be traced, and to provide a summary of the available literature. It is presented as an annotated chronology so that the history of the various concepts can be followed. 'Non-scientific' publications have been included because few of the more contentious issues have been committed to refereed literature, but the ideas expressed are important in the context of this thesis.

2.1 Annotated chronology of previous work on *Harpagornis moorei*

1869 - Haast: describes the type locality at Glenmark for the first time

1871 - Haast: paper describing *Harpagornis moorei* read at May meeting of Canterbury Philosophical Society, Christchurch

1872 - Haast: description of *Harpagornis* Haast, and *Harpagornis moorei* Haast from left femur, one thoracic rib, and an ungual pedal phalanx; mentions further specimens from two other, apparently older, sites in the same valley

1873 - Grey: suggests that a Maori legend of extinct bird of prey Hokioi referred to *Harpagornis moorei*

1874 - Haast: refers more material from Glenmark to *Harpagornis moorei*, and describes second species, *Harpagornis assimilis*, from most of the skeleton of a smaller bird found near the first site, with reservations that it probably represented the smaller male of *H. moorei*

1875 - Booth: describes a new site for *Harpagornis moorei* at Hamilton Swamp, near Ranfurly in Central Otago

- Haast: lists artefacts found at Moa Bone Point Cave, Sumner, near Christchurch, including an "awl" fashioned from the distal end of a tibiotarsus attributed to *Ossifraga gigantea* [= *Macronectes giganteus* or *M. halli*]; name crossed out in pencil and marginal emendation "*Harpagornis*" added in Hutton's hand in Canterbury University library copy (Hutton's copy)
- Hector: Untitled notice of Hector's exhibition of pelvis from 'Cowes', in the Obelisk Range, Central Otago, at a meeting of the Zoological Society, London; now in BM(NH)
- McKay: mentions traditions of the *Hokioi*
- Owen: describes and illustrates several major bones from casts and photographs supplied by Haast; suggests that the bird was a hunter, and that it flew well but had a proportionately short ulna

1879 - Haast: narrative of Glenmark expeditions; detailed descriptions of Glenmark sites, including type sections for *Harpagornis moorei* and *H. assimilis*, and location of other sites in valley from which other fragments of eagle bone were collected; describes sightings of large raptors in valleys of the Southern Alps that Haast speculates may have been *Harpagornis moorei*

- Owen: memoir of 1875 republished, which plates, as part of volume of his collected works on the flightless and other birds of New Zealand

1880 - Colenso: provides further comments on the Maori legend of the *Hokioi* as the extinct eagle

1881 - Haast: describes material from the site at Hamilton Swamp discovered and described by Booth

1882 - McKay: describes a new site at Motunau, North Canterbury, with moa bones; site was beneath gravels and associated with peat and remains of trees

1883 - Hector: notice of the discovery at Motunau in Geological Survey Report for 1882

- McKay: repeat of McKay (1882) and Hector (1883)

1884 - Quatrefages: a mention in passing that the eagle was called *weka* by the Maoris

1889 - Hamilton: lists two new sites, both in the North Island; Puketapu and Te Aute, but does not give details of material found

1891 - Lydekker: list of material in BM(NH), including casts, and first mention of first phalanx of major digit of the right wing found by W. Mantell, ostensibly at Waingongoro, on the southern Taranaki coast in the late 1840s, the first bone of the eagle to be collected; lists *Harpagornis assimilis* as a synonym, with (?)

1892 - Forbes: describes a new swamp site at Enfield, near Oamaru; many eagle bones found; bones not listed

1893 - Gadow: lists *Harpagornis moorei* from the Pleistocene of New Zealand, placed in his Falconidae, some dimensions of long bones

- Hamilton: describes the site at Castle Rocks, western Southland; list of material from there, and all other material known to him at that time; figures a cranium; lists a tarsometatarsus from Dunstan Range, and another from "Maori middens" at Warrington

1894 - Buller, L. Translation of Quatrefages' paper

- Hamilton: further material from Castle Rocks; nearly complete skeleton referred to *Harpagornis assimilis*; illustrations of skull, sternum, and provides some dimensions

1896 - Hutton: lists one tibiotarsus from a new swamp site at Kapua, near Waimate

- Hutton: description of the site at Enfield; points out that Forbes had taken the Enfield material to England

- Shufeldt: letter to T J Parker at Otago outlining results of comparisons of photographs of material with other raptors; *Harpagornis* represents "a more generalised aquiline type, and might easily have been the common ancestor to a number of" modern genera

1897 - Drew: lists material attributed to *Cnemiornis* and moas from site near Hunterville [makes no mention of *Harpagornis* but Millener (1981) suggests that the material included *Harpagornis*

- Parker: nearly complete skeleton sluiced from a gold mine [Golden Point] at Deep Dell Creek, near Macrae's Flat, inland from Dunedin; mentions that it was deposited in the Otago University Museum
- Hutton: list of material found in the Glenmark deposits; and notes on the deposit

1898 - Beddard: *Harpagornis* from the New Zealand Pleistocene was 1.5X the bulk of a golden eagle, belonging to the same division of the Accipitres

- Parker: exhibited and commented on mounted specimen of *Harpagornis* collected at Castle Rock [collected by A Hamilton]; he deposited it in Otago University Museum
- Stack: relates the legend of the *Pouakai*, a giant predatory bird

1899 - Newton: *Harpagornis* was large enough to prey on the largest *Dinornis* moas

1904 - Hamilton: subfossil bones found at a fissure site at Ngapara, inland from Oamaru; site described and species listed

1907 - Rothschild: repeats descriptions from Haast, with dimensions; distinguished from *Aquila* by ulna being relatively shorter, and the stouter tarsometatarsus

1921 - Franz: height 1 m; wing span 3 m [quoted (in German) in Lambrecht 1933]

1924 - Hesse: there is even a flightless bird of prey in New Zealand [quoted (in German) in Lambrecht 1933]

1930 - Oliver: described both nominal species separately; photograph of mounted skeleton in Otago Museum; closely allied to *Aquila*, but distinguished by the narrow skull, short ulna; stout tarsometatarsus distinctive; femur longer than tarsometatarsus, as in *Aquila*

1931 - Buick: [also 1936, 1937] mentioned in books on the moa as a predator on moa chicks

1933 - Lambrecht: repeats generic diagnosis from Oliver (1930); literature survey; history of discovery, etymology of name, important sites, material; assimilis is probably the male; summary of Haast's and Owen's comments on relationships; measurements

1941 - Archey: scavenging of hawks or even the attacks of the extinct eagle *Harpagornis* may possibly account for the missing heads and necks of moas in swamps at Pyramid Valley and Te Aute

1942 - Falla: one terminal ungual phalanx from the Wairau Bar excavations; not numerically well represented; points out that association with human remains was also noted by Hutton, who corrected label and annotated Canterbury Museum copy of Haast's paper about the distal tibiotarsus artefact from Sumner; suggests that the Sumner artefact appears to have been made from fresh, and not subfossil, bone

1945 - Oliver: Shufeldt placed *Harpagornis* near *Aquila*; skull form indicates that it is nearer *Haliaeetus*, indeed further from *Aquila* than is *Haliaeetus* [contra his 1930 comments]; the broad sternal notches are primitive, and the ilio-ischiadic surface of the pelvis differs from the normal condition in eagles

1948 - von Haast: anecdotes from Haast (1879) and about Owen's comments on Haast's work; describes the fate of the bird's discoverer, F Fuller

1949 - Dawson: *Harpagornis* listed from the dunes at the southern end of Grassmere Spit, [= Marfells Beach] Marlborough

- Duff: a close relative of the Wedge-tailed Eagle of Australia; lateral view of skull and mandible; pictorial reconstruction as a Wedge-tailed Eagle

1951 - Duff: resembles the Wedge-tailed Eagle, but has reduced wing bones and longer legs, showing tendency towards flightlessness; almost certainly did fly; wing span probably nearly that of the

Wedge-tailed Eagle; among the rarest of all the extinct birds; two skulls found during the 1949 Pyramid Valley 'digs'; eagles may have been trapped in swamps while feeding on trapped moas; contemporaneous with the earliest Polynesians in New Zealand

1952 - Duff: reprinted

1953 - Fleming: a basic chronology for the north-eastern part of the South Island, based on presence or absence of human material with bird remains, including eagle

1955 - Oliver: both species briefly described [largely as in Oliver (1930)], with localities, in the family Falconidae; closely allied with *Haliaeetus* [rather than *Aquila*]; narrow skull, short ulna, and stout [tarso]metatarsus; photograph from 1930 edition

\- Scarlett: *Harpagornis* added to the Pyramid Valley list

1956 - Duff: reprint of Duff (1949); illustrations of artefacts made from eagle bone, found at Sumner and the Wairau Bar; made from distal tibiotarsi and ulnae

1961 - Dawson: an extinct sea eagle from the Chatham Islands is very different, at least in size, from *Harpagornis*

1964 - Brodkorb: listed in the subfamily Buteoninae; *Harpagornis assimilis* a synonym

1969 - Scarlett: eagle first found at Glenmark; very large, robust, and thick-set; it preyed on moas and probaly went extinct when the moas died out; known to Polynesians and artefacts made from its bone; scarce, judging from scarcity of finds

\- Wilson: listed from King's Cave, South Canterbury, but not from Metro Cave on the West Coast

1970 - Kinsky: listed in appendix; *Harpagornis assimilis* a synonym, based on the male; found in association with human sites

1972 - Scarlett: illustratedn major bones, with dimensions for 11; food given as moas

1973 - Grant-Mackie & Scarlett: listed from an Oturian interglacial site in the Hillgrove Formation at a beach south of Oamaru [Old Rifle Butts]

- Harrison & Walker: *Harpagornis moorei* has been described from Quaternary of New Zealand; tarsometatarsus with characters such as double calcaneal ridge, and shorter trochlea for digit 2 suggesting affinities with typical *Aquila* eagles; not [their] *Ichthyophaga australis* from the Chatham Islands

1979 - Scarlett: listed from Lake Grassmere

1981 - Millener: reviews sites and history of discovery; cites type locality as Glenmark, near Oamaru; types held at National Museum; in South Island recovered from five caves, seix swamps, three dune/middens, and late Pleistocene sands; refutes Motutapu and Great Exhibition Bay records, (*Pelecanus* and *Ovis aries* respectively), leaving four North Island sites; cites King (1969) presumably Wilson (1969) for King's Cave mentioned; disputes most evidence for contemporaneity with Polynesians

1982 - McCulloch: eagle and other birds victims of man's activities; extinction of moa removed eagle's food supply; evidence suggests that eagles scavenged on moas trapped in caves and swamps; line drawing reconstruction as a forest eagle (D H Brathwaite)

1984 - Millener (1984a): popular account of discovery of eagle material at Honeycomb Hill Caves; nearest relative is the Wedge-tailed Eagle; spent much time on the ground, and fed largely on carrion; type locality Glenmark, near Oamaru; weight up to 18 kg, wingspan to 2.5 m; much more powerful legs and relatively shorter wing bones than the Wedge-tailed Eagle; sternal keel much shallower than in that species

- Cassels: survived by the comparable Wedge-tailed Eagle of Australia; indicates some characteristics in common with other extinct New Zealand birds, such as large size, low clutch size

- Millener (1984b): bone accumulations in caves not attributable to predators; eagle is very rare in deposits; very good material recovered from several sites within the extensive cave system at Honeycomb Hill, Oparara; up to 18 kg, and 2.5 m; found in only 20 sites (four in the North Island); at least 7 individuals at Honeycomb Hill
- Trotter & McCulloch: an indirect victim of man's invasion; rare in archaeological sites, and probably not important as human food; largely a carrion eater, with diminished powers of flight; found in swamps and sinkholes with remains of moas on which it fed

1985 - Temple & Gaskin - included in popular story of the life of a large moa near Pyramid Valley

1987 - Brewster: could have been a major predator on (mainly young) moas; up to 13 kg, 2.6 m wingspan; particularly large rear claw; at least 20 eagles recovered from Oparara (Honeycomb Hill); rare

- Worthy: Otiran deposits from the Graveyard and from the Eagle's Roost, Honeycomb Hill Caves; tomo acted as a pit trap; listed associated species; described vegetation change with time, and absence of eagles from area when open montane forest was replaced (in the Holocene) by dense, wet forest; preferred open grassland or scrubland; had to be able to see prey on the ground while flying; at least 11 individuals represented three sites; sample from these caves equal to one-third of that from all other sites
- Brathwaite & Holdaway [abstract]: brief summary of weight estimates and ecology
- Brathwaite: (*Press*) probable size and ecology
- Brathwaite: (*Evening Post*) probable size and ecology
- Holdaway: (Press 9 June: 29), probable size and ecology

1989 - Holdaway: (*New Zealand geographic 4*: 56-63) history of discovery and ideas on biology

1990 - Manning: (*Nelson Evening Mail* 11 Jan: 1) discovery of Mount Owen specimen; photograph of first elements removed

- Lynch: (*Dominion* 12 Jan: 1) discovery of Mount Owen specimen; photograph of skull; painting reconstructed as forest eagle
- [Anonymous] (*Marlborough Express* 12 Jan: 1) discovery of Mount Owen specimen; photograph of skull; drawing of bird chasing a pukeko
- Metcalfe: (*Press* Jan 13: 9) discovery of Mount Owen specimen
- [Anonymous] (*Nelson Evening Mail* Jan 15: 9) excavation of Mount Owen specimen
- Lynch: (*Dominion* Jan 16) Recovery of Mount Owen specimen
- [Anonymous] (*Evening Post Jan 17)* Discovery of Mount Owen specimen; photograph of assembled foot bones in comparison with that of *Circus approximans*
- [Anonymous] (*Otago Daily Times* Jan) recovery of Mount Owen specimen and history of Castle Rocks specimen in Otago Museum; photograph of Otago specimen

1991 - McCulloch (*Press* Jan 3: 13)- restated carrion-eating hypothesis

- Stevens, G R *et al.* (in press) Wingspan 3 m; weight 15 kg; extinct about 500 years ago; painting of forest eagle in open country with grazing moas.

3. STRATIGRAPHIC TERMS AND CONVENTIONS

In this study, I maintain the distinction between Holocene and Pleistocene for convenience in distinguishing between the climatic and vegetation regimes of the Otiran glacial maximum and those existing through most of New Zealand over the past 10 000 years, and for consistency with recent usage.

Although the climate began to ameliorate about 14 000 years ago and forest rapidly expanded in the North Island (Newnham *et al.* 1989), reafforestation was not complete in the South Island until about 10 000 years BP (Burrows 1979; McGlone 1988, 1989). 14 000 years BP is recognised by, for example, Burrows (1984) as the start of the Aranuian Interglacial, but much of the recent literature on New Zealand Quaternary vertebrate faunas, vegetation, and climate (e.g., Anderson 1983; Bussell 1988; McGlone 1988; Millener & Templer 1981; Worthy & Mildenhall 1989) uses Holocene rather than late Quaternary. The term is still in wide use, even if no clear boundary section can be defined (e.g., Purdue 1989).

The last glacial maximum of the Otira glaciation, which lasted from about 22 000 to 14 000 years BP, is referred to here briefly as the Otiran. Few sites containing eagle or other bird bone have been dated at older than 24 000 years. Older sites certainly exist, and some of these may be as old as the Oturian Interglacial (Grant-Mackie & Scarlett 1973), about 80 000 years BP.

The divisions used here, and the normal range of ages of different kinds of sites are summarised in Fig. 3.1.

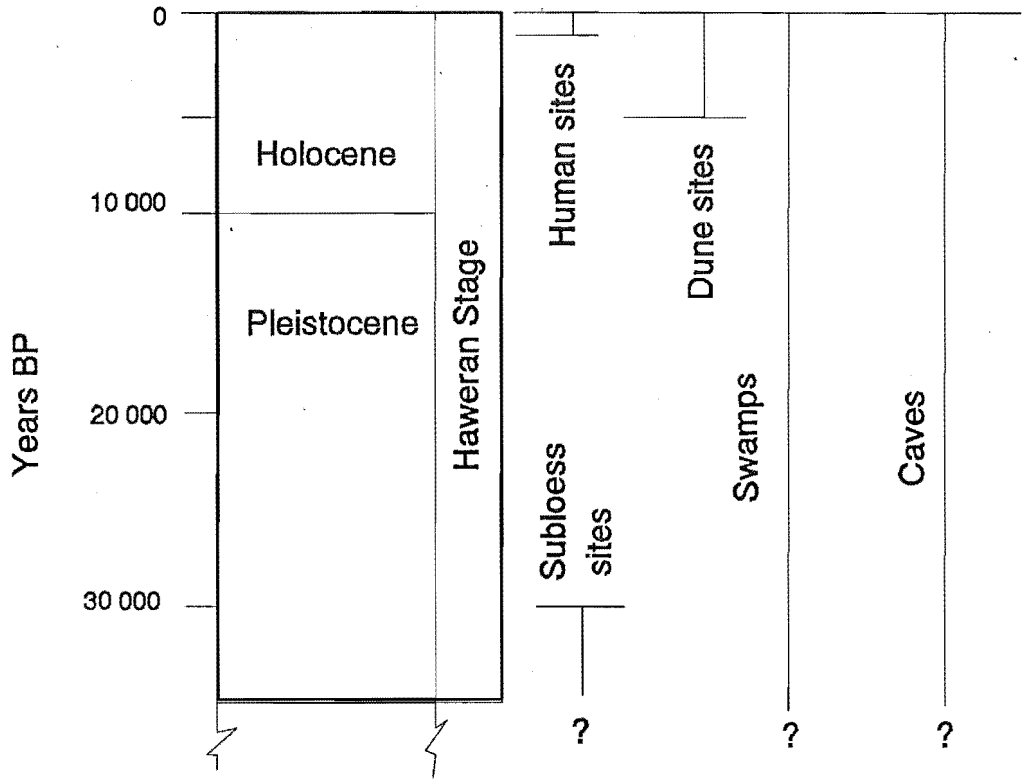

Fig. 3.1 Diagram showing time scale and terms used in this study, and approximate ranges of dates for different kinds of sites containing eagle bones in New Zealand.

4. GENERAL METHODS

Only methods basic to the whole study are presented here; methods specific to a particular chapter are dealt with after the Introduction to that chapter.

4.1 Bones

For the most part, bones were examined as they were; no specialised preparation techniques were used or necessary. Some bones required the careful removal of calcareous deposits, and a few were repaired using Bostik®, an adhesive that is readily removed by acetone. No field collecting was done. All existing material had either been found serendipitously, at long intervals, or during major field work at large fossil deposits.

Many of the classic sites that produced eagle bones have either been destroyed, or cannot now be located. During the period of my study, continuing excavations of deposits in the Honeycomb Hill system of caves near Karamea by National Museum of New Zealand parties brought to light much new material. This greatly helped my work, because the material included many small and fragile elements that previously were not represented in collections.

Luck plays a big part in any palaeontological endeavour, but the discovery of the unequivocally associated elements of an almost complete skeleton in a cave near the top of Mount Owen, southwest of Nelson in January 1990 was exceptional. This skeleton allowed previous work to be checked, new insights, provided a firm basis for attribution of unassociated material to the taxon, and was the basis of my redescription after its taxonomic identity was confirmed by comparison with the type material.

4.2 Institutions

The institutions housing material used in this study, and abbreviations used in the text (collection number code in parenthesis), are: NZAIM (AIM), Auckland Institute and Museum, Auckland, New Zealand; BMNHP (various), British Museum (Natural History), Palaeontology Department; BMNHT (various), British Museum (Natural History) Sub-Department of Ornithology, Tring;

NZCM (AV), Canterbury Museum, Christchurch, New Zealand; NMNH (USNM), National Museum of Natural History, Smithsonian Institution, Washington, D.C.; NMNZ (DM or S), New Zealand National Museum, Wellington, New Zealand; NZNO, North Otago Museum, Oamaru, New Zealand; MZOM, Otago Museum, Dunedin, New Zealand; NZSM, Southland Museum and Art Gallery, Invercargill, New Zealand.

4.3 Figures

Figures were prepared for several purposes: indication of mensural landmarks; description of bones; details of features used in phylogenetic analysis and bone description; structural and force diagrams. Base drawings were made from transparencies via a camera lucida attachment on a Wild M7 binocular microscope (mag. range 10-20), or traced directly from projections of negative images enlarged to an appropriate scale, without correction for parallax error.

The scale of each drawing was determined both by the dimensions of the bone or structure, and the degree of detail required. Some distortion of shapes and planes was unavoidable when the bone or its image was so large as to require several part drawings assembled as a whole. The distortion was not usually excessive.

4.4 Photographs

Monochrome photographs were taken on Ilford FP4 and Kodak Tmax 100 film (E.I. 100/21°), using natural light or a custom-built light box. A Minolta SRT-101 35 mm single lens reflex camera was used, with a standard 55 mm lens and through-the-lens light metering. Lens extension tubes were used for a few close focus shots. Exposures varied according to conditions for natural lighting, but was always 1/8 s at f16 in the light box, without use of extension tubes.

The box was used for all exposures of stereo pairs for plate production. FP4 film was developed in Ilford ID-11 developer for 6.5 minutes; 1 roll of Ilford PanF stock was developed in ID-11 for 6 minutes; and Kodak TMX stock was developed in Kodak TMAX developer for 6.5 minutes. Prints were made on Agfa MC 310 RC glossy paper, developed in Ilford Bromophen for 2 minutes.

Plates were prepared by cutting around each image, fixing image sets to black card, and rephotographing with 35 mm Tmax film. These negatives were then printed on Agfa Copyline projection P 90 paper. Results of trials using direct photography as screened bromides, xerography of the primary prints, and composite primary print plates were unsatisfactory. A black ground was preferred.

4.5 Measurements

The measurement landmarks used are shown in Fig. 4.1. All measurements were made with Vernier callipers, to the nearest 0.1 mm. For some measurements, the bone was held in the appropriate orientation against a flat surface, and the measurement made to that surface, rather than to the bone itself; such measurements are indicated by an asterisk (*) on Fig. 4.1. Where a bone surface was slightly worn or abraded, measurements are minimum values, and were used only if the estimated loss of surface was ≤ 1 mm. Measurements were not taken if more significant damage was apparent. Where a dimension was estimated by reconstruction of a surface, or process for a specific purpose, this is noted in the text. Estimated dimensions were not included in statistical treatments, or summaries of bone dimensions. Because some bones were damaged on some, but not all, surfaces, they are not represented in all data sets. Sample sizes therefore vary, and are not necessarily the same as the total number available of a particular element.

4.6 Cartographic conventions

Sites that had yielded eagle bones were located from literature references, unpublished reports, museum labels and catalogues, and from personal contacts with collectors. Most sites in the South Island were visited and photographed, and exact collection sites examined if they still existed. Notes were made about the adjacent terrain, slope, aspect, and exposure of the site, as well as the mode of deposition, and the excavation or collection techniques used there. The positions of sites were noted to the nearest 100 m if possible, or to the greatest

accuracy permitted by available information. Some sites have never been fully described or localised and could be identified only as general localities.

Site locations are described by latitude and longitude, altitude, and by map coordinates from both the NZMS 1 (1:63 360) and NZMS 262 (1:50 000) map series, where sheets both were available. Altitudes were estimated to the nearest 50 m (160 ft) from the latest edition of the appropriate 1:50 000 (NZMS 260) or 1:63 360 (NZMS 1) sheet.

4.7 Literature

The literature on New Zealand fossil birds is relatively compact. Most work has been published in New Zealand or England in English-language journals, and much of it is readily available in local libraries. However, a distressingly large amount of recent research has appeared only in unpublished theses and commissioned reports and is not available in peer-refereed journals. I have used such material where necessary, but with strong misgivings because of its limited availability. Anecdotal comments have been included because they constitute much of the literature on Haast's eagle. Unfortunately, the publication of unsubstantiated anecdotes has perpetuated misconceptions about the bird and introduced new errors to the literature, as will become apparent.

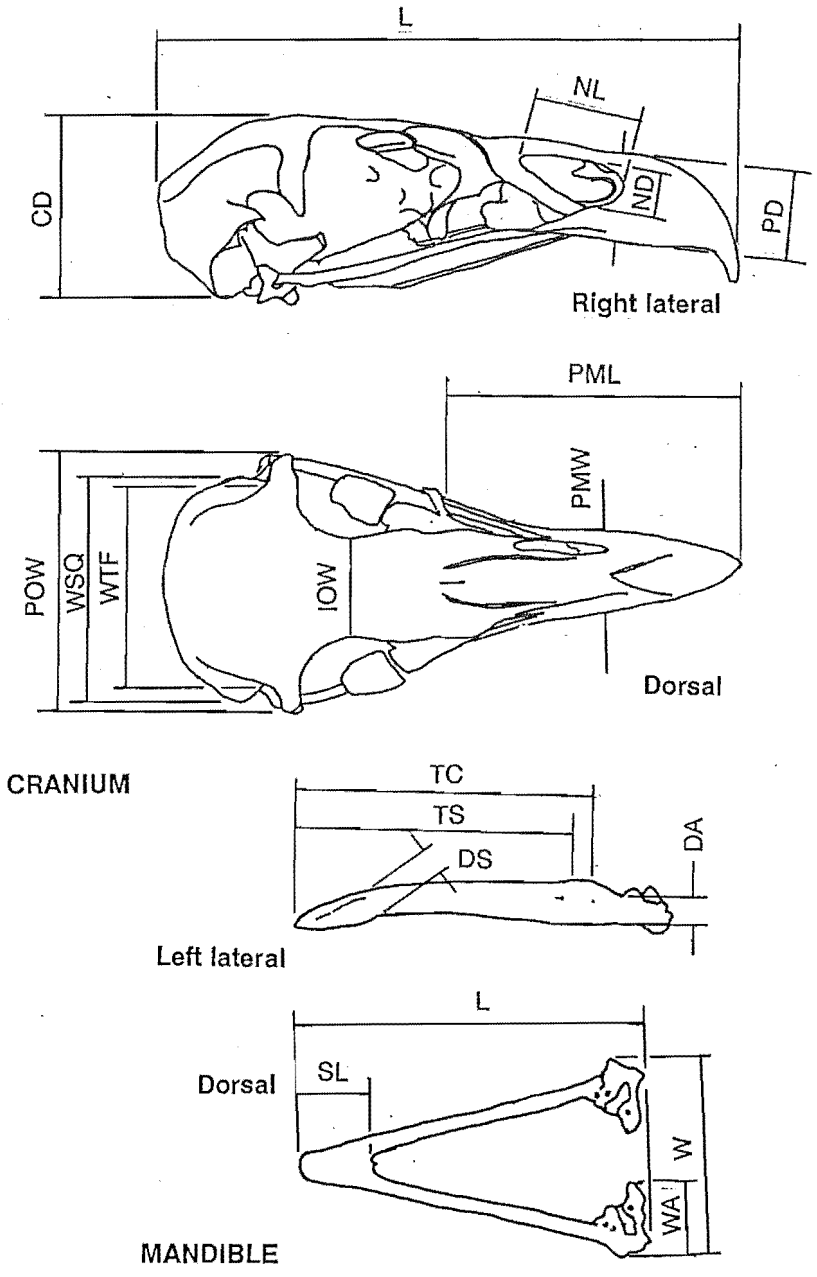

Fig. 4.1 (A-F) Measurement landmarks and dimensions for elements. A, cranium, premaxilla, and mandible. Not to scale. Cranium and premaxilla: L, length; CD, cranial depth; PD, premaxilla depth; NL, naral length; ND, naral depth; PML, premaxilla length; POW, postorbital width; WSQ, width across squamosals; WTF, width across temporal fossae; IOW, interorbital width; PMW, premaxilla width. Mandible: TC, tip to coronoid process; TS, tip to surangular process; DS, depth at proximal end of symphysis; DA, depth anterior to articular process; L, overall length; SL, symphysis length; W, overall width; WA, width of medial articular process.

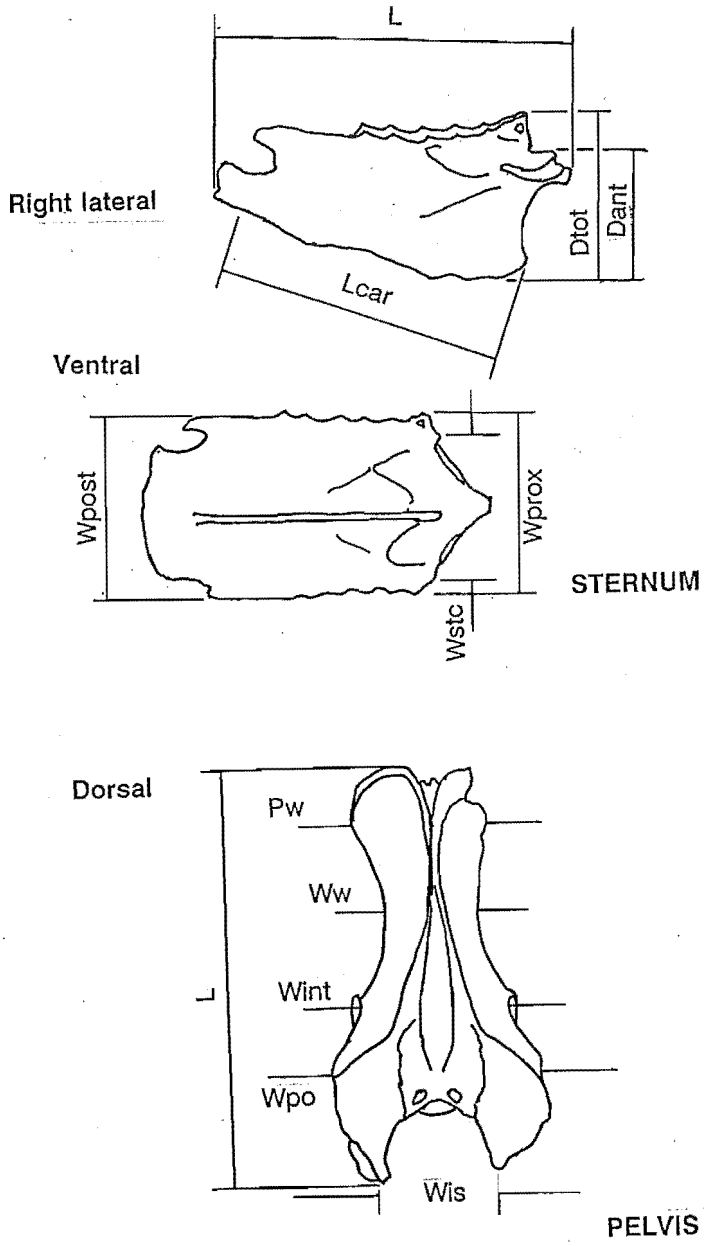

Fig. 4.1B Measurement landmarks and dimensions for elements: sternum and pelvis. Not to scale. Sternum: L, total length; Dtot, total depth; Dant, anterior depth; Lcar, length of carina (keel); Wprox, total proximal width; Wpost, total posterior width; Wstc, width across sterno-coracoidal processes. Pelvis: L, length; Pw, proximal width; Ww, width at 'waist'; Wint, width across acetabuli; Wpo, width across maximum extent of posterior ilio-ischial crest; Wis, width across posterior extremities of ischia.

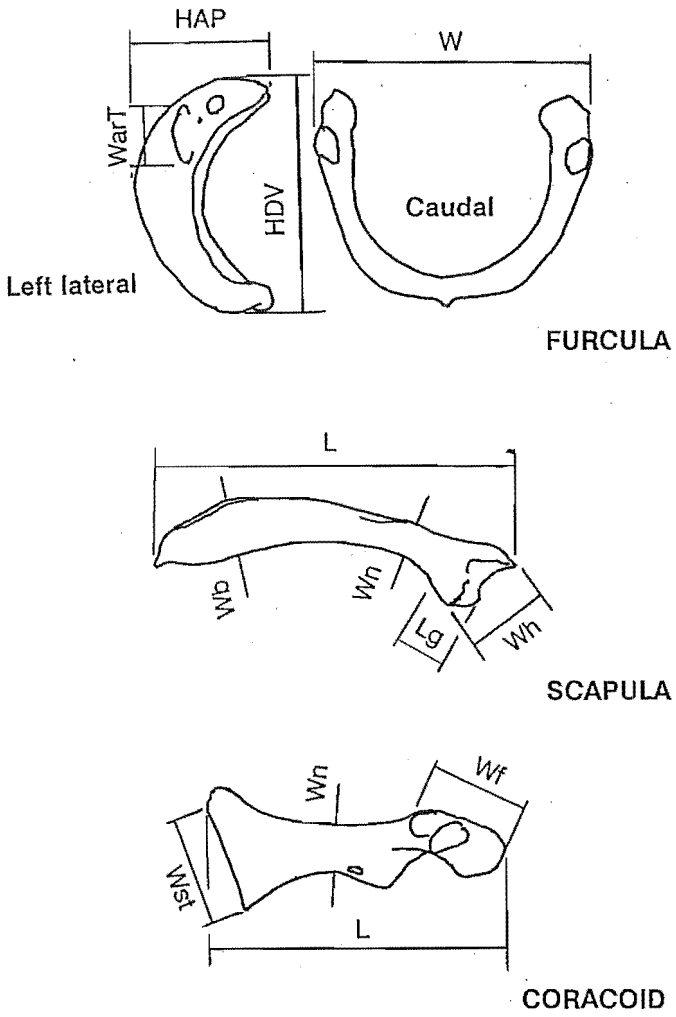

Fig. 4.1C Measurement landmarks and dimensions for elements: furcula, scapula, and coracoid. Not to scale. Furcula: HAP, 'height' from anterior margin to line connecting posterior extremities; W, total width; WarT, width of articular facet; HDV, dorso-ventral height. Scapula: L, length; Wb, maximum width of blade; Wn, width of neck; Lg, length of glenoid facet; wh, width of head. Coracoid: Wf, width of furcular facet; Wn, width of shaft; Wst, width across sternal facet; L, length (to end of sternal facet).

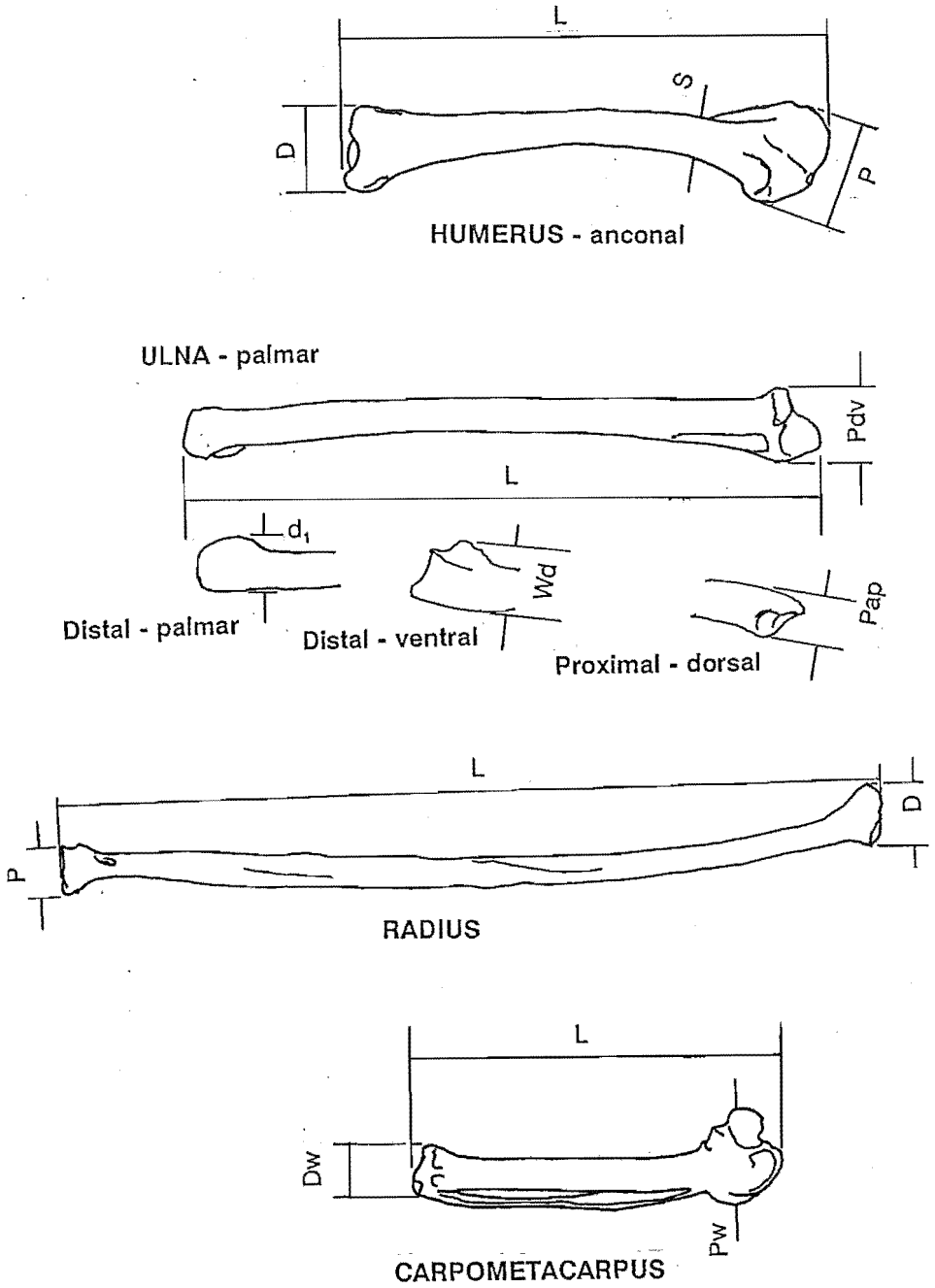

Fig. 4.1D Measurement landmarks and dimensions for elements: humerus, ulna, radius, and carpometacarpus. Not to scale. Humerus: L, length; D, distal width; S, shaft dorso-ventral diameter at distal end of deltoid crest; P, proximal width. Ulna: L, length; Pdv, proximal dorso-ventral width; d_1, width across distal surface; Wd, distal width, across process; Pap, proximal antero-posterior width. Radius: L, length; P, proxiaml width; D, distal width. Carpometacarpus: L, length; Dw, distal width; Pw, proximal width.

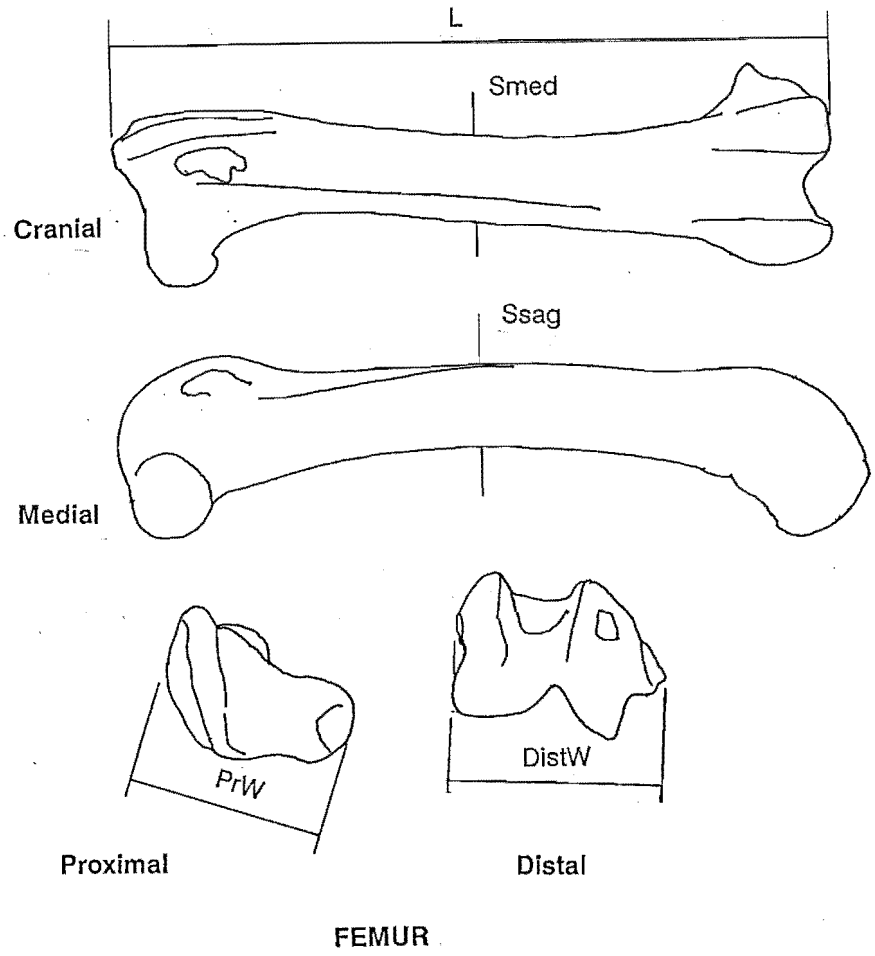

Fig. 4.1E Measurement landmarks and dimensions for elements: femur. Not to scale. Femur: L, length; Smed, mid-shaft medial diameter; Ssag, mid-shaft sagittal diameter; PrW, proximal width; DistW, distal width.

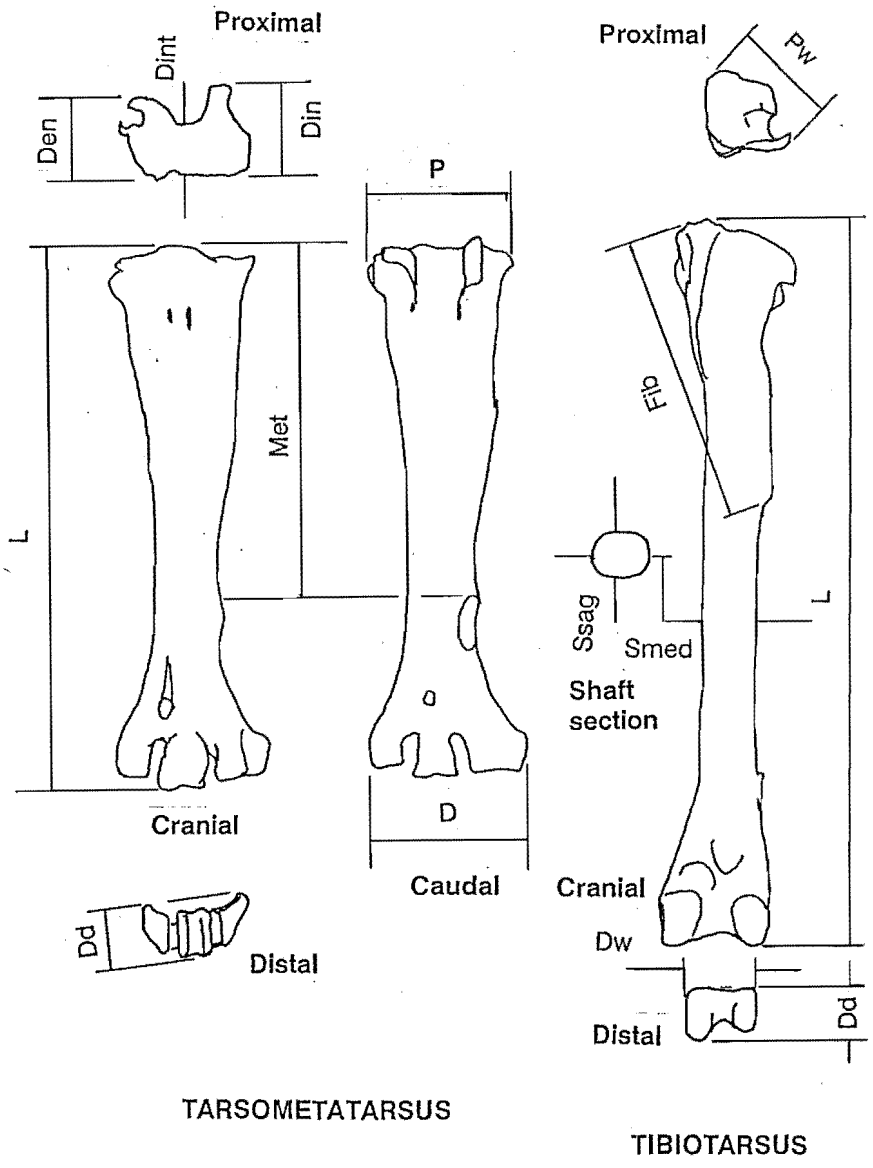

Fig. 4.1F Measurement landmarks and dimensions for elements: tibiotarsus and tarsometatarsus. Not to scale. Tarsometatarsus: Dint, shaft depth between hypotarsal ridges; Den, depth over medial hypotarsal ridge; Din, depth over lateral hypotarsal ridge; P, proximal width; L, length; Met, proximal end to fossa of first metatarsal; D, distal width; Dd, distal depth. Tibiotarsus: Pw, proximal width; Fib, proximal end to distal end of fibular crest; L, length; Ssag, mid-shaft sagittal diameter; Smed, mid-shaft medial diameter; Dw, distal width; Dd, distal depth.

CHAPTER 1

5. CHAPTER 1
AN EXPLORATORY PHYLOGENETIC ANALYSIS OF THE ACCIPITRIDAE

5.1 INTRODUCTION

The history of the taxonomy and systematics of the Falconiformes [=Accipitriformes] has been reviewed at length by Sibley & Ahlquist (1972) and Jollie (1976, 1977a, 1977b, 1977c). They included extensive literature citations and comparisons of previous classifications, and these will not be repeated here. There is general agreement that relationships between groups within the family are not understood (de Boer & Sinoo 1984; Jollie 1976, 1977a, 1977b, 1977c; Olson 1985). The fossil history of the Accipitridae was reviewed by Olson (1985), who emphasised the problems of incorporating fossil accipitrids into present classifications based on external morphological characters.

Haast (1872), Owen (1879), Shufeldt (1896), and Oliver (1930, 1945, 1955) were hampered by the lack of a sound classification and information on variation in skeletal morphology when they assessed the relationships of *Harpagornis moorei*. Fürbringer's (1882) monumental treatise on avian systematics was not available to earlier workers, and osteological characters have been omitted from most later diagnoses and systematic treatments (Amadon 1953, 1964, 1978, 1982a, 1982b; Brown & Amadon 1968; Friedmann 1950; Stresemann 1979). The works of Beddard (1889, 1898) and Suschkin (1899, 1900, 1905) were limited in coverage, or not readily available to southern hemisphere workers.

Osteological diagnoses of subfamilial groups in the Accipitridae are often ambiguous, and most descriptions and diagnoses of families and subfamilies rely on external characters (Witherby *et al.* 1939): identical osteological characters have even been offered in diagnoses of different groups (Friedmann 1950).

At higher taxonomic levels, the basic problem has been that the order, as generally conceived (e.g., Brown & Amadon 1968; Stresemann & Amadon 1979), includes diverse groups whose profound differences have been appreciated for over 100 years (Beddard 1898; Friedmann 1950). Jollie (1953) pointed out why the group should be considered to be polyphyletic, as a counter to Clay's (1951)

suggestion that the order was monophyletic. Clay based her proposal on the distribution of several genera of bird lice (Mallophaga) on hosts in the different bird families.

As listed by Stresemann & Amadon (1979), the Falconiformes includes four suborders: Cathartae (Vulturidae [Cathartidae *auct.*]; the 'New World' vultures); Accipitres (Accipitridae; hawks, eagles, kites and Old World vultures); Sagittarii (Sagittariidae; *Sagittarius serpentarius*); and Falcones (Falconidae: falcons and caracaras). The Accipitridae of Stresemann & Amadon (1979) contained two subfamilies: Pandioninae (the osprey (*Pandion haliaetus*); and Accipitrinae.

There is compelling osteological (Emslie 1988; Jollie 1976, 1977a, 1977b, 1977c; Ligon 1967; pers. obs.), karyological (de Boer 1976), and behavioural (König 1982) evidence that the Vulturidae are related to the storks (Ciconiidae) and do not belong with the accipitrids. This was recognised by Friedmann (1950), Brown & Amadon (1968), and Amadon (in Stresemann & Amadon 1979), but was not followed in the classifications of any of these workers.

The karyotype of Falconidae differs from that of the Accipitridae (de Boer 1976), and Jollie (1976, 1977a, 1977b, 1977c) concluded on osteological, pterylogical, and other morphological grounds that the Falconidae are not related to the accipitrids.

Neither the falcons nor the New World vultures are considered further here. However, I have included *Sagittarius* as an outgroup for analysis of the relationships within Stresemann & Amadon's (1979) Accipitrinae. *Pandion* was included because it was included in their Accipitridae, although other authors have accorded it familial (Brown & Amadon 1968) or even subordinal (Hudson 1948) rank.

Amadon (in Stresemann & Amadon 1979: 272) declined to recognise any formal divisions *within* their Accipitrinae, although Stresemann in the original manuscript had recognised eleven. There is no better indication of the uncertainty in the knowledge of the relationships within the Accipitridae.

de Boer (1975, 1976) and de Boer & Sinoo (1984) have stressed the uniqueness of the accipitrid karyotype, which strongly suggests that the group,

excluding *Pandion* and *Sagittarius*, is monophyletic. The problem, therefore, was to determine the sister group of *Harpagornis moorei* within an apparently homogeneous assemblage of about 220 species.

5.1.1 Phylogenetic analysis

Jollie (1976, 1977a, 1977b, 1977c) rejected as inappropriate the use of phylogenetic (cladistic) techniques in his systematic work on the Accipitridae. His was one of two recent attempts to produce a non-linear arrangement of species within the Accipitridae, both of which left open the connections between major branches (Brown & Amadon 1968; Jollie 1976, 1977a, 1977b, 1977c).

Like Raikow (1985) I believe that the traditional eclectic systematic method, as used by Amadon (1953, 1964, 1977, 1978, 1982a, 1982b, Brown & Amadon 1968, Stresemann & Amadon 1979), Brown (Brown 1982; Brown & Amadon 1968), Jollie (1976, 1977a, 1977b, 1977c), and Stresemann (Stresemann & Amadon 1979) cannot generate a classification based on phylogeny.

According to Raikow (1985), a classification must be unambiguous in the information content of taxa and categories, and therefore consistent in the way taxa are recognised and ranked. Grades of development should not be recognised taxonomically. "The rank of all taxa should be determined according to one system so that the nature of the relationship between any taxa of the same or different rank will be automatically designated" (Raikow 1985: 189). Phylogenetic and phenetic methods can produce such classifications, but eclectic techniques do not (Raikow 1985).

I rejected the phenetic approach of seeking a measure of overall similarity as inappropriate because there was strong evidence for convergence (e.g., between *Ictinia* and the *Elanus* kites (Shufeldt 1896)) in the Accipitridae. I used phylogenetic analysis because it is based on the assumption that shared derived characteristics are the best indicators of common ancestry (Hennig 1966; Wiley 1981). The use of derived characters reduces the effects of shared primitive features (symplesiomorphies) and of convergent features (homoplasies) (Wiley 1981). The development of several computer programs (e.g., PHYLIP,

MACCLADE, PAUP) have simplified the analysis of large character suites for many operational taxonomic units (OTUs).

The principal aims of the work reported in this chapter were to identify a sister group for *Harpagornis moorei* among the genera of the Accipitridae, and to produce a preliminary hypothesis of the phylogeny of the Accipitridae based on osteological features.

5.2 METHODS

5.2.1 Taxa and specimens

A full survey of all species in the Accipitridae was not attempted. Instead, each monotypic genus and one or more representatives of polytypic genera were studied. Some genera of Accipitridae are not well-defined, for example there is considerable discussion as to the limits of *Aquila, Accipiter,* and *Gyps* (Amadon & Brown 1968; Amadon, in Amadon & Stresemann 1979: Amadon 1978, 1982a). Where possible, one of the best known members of large genera was chosen to represent the genus.

I examined skeletal material of *Pandion haliaetus, Sagittarius serpentarius,* and 66 species representing 51 of the approximately 60 genera and 215-220 species presently included in the Accipitridae. Eight genera were represented by two species, and one genus by three species (Table 5.1).

Table 5.1 Material examined for phylogenetic study of the Accipitridae, listed alphabetically within families.

Institutions: BMNH, Sub-department of Ornithology, British Museum (Natural History) - now Natural History Museum - Tring, England (no prefix to specimen number); NMNH, National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. (all numbers prefixed USNM); NMNZ, National Museum of New Zealand, Wellington, New Zealand (numbers prefixed S).

SPECIMENS

Pandionidae

Pandion haliaetus, 1851.11.10.65, incomplete; *Pandion haliaetus carolinensis*, ♂, USNM 18466, Chesapeake Bay, captivity, 3 Jan 1969; *Pandion haliaetus carolinensis*, USNM 851, Carlisle, Pennsylvania.

Sagittariidae

Sagittarius serpentarius, S/1952.3.198, South Africa; USNM 321578, Cape of Good Hope, South Africa, Sep 1865.

Accipitridae

Accipiter nisus, ♂, S/1987.31.1, Witley, Surrey, England, 9 Aug 1987; ♀, immature, 1910.10.2.1, 12 Oct 1910; ♀, USNM 554271, Assen, Holland, 15 Feb 1979; Aegypius monachus, 1872.10.25.5; ♀, USNM 428040, captivity, 29 Aug 1949; *Aquila audax*, ♀, 1898.5.7.6, Sydney; *Aquila chrysaetos*, S/1973.66.57, captivity; ♂, adult, USNM 491476, Alaska, 1973(?); *Aviceda leuphotes*, 1845.1.12.30, Nepal; *Aviceda subcristata rufa*, ♀, Obi Besar, Moluccas, Indonesia, 29 Jul 1982; *Busarellus nigricollis*, ♂, 1895.3.10.7, 6 Sep 1895 [first identified as *Heterospizias meridionalis*: note by P Suschkin in box, changing identification]; USNM 345773, between Caceres and Concepcion, 6 Oct 1940; *Butastur liventer*, 1850.8.15.79, Java; *Butastur indicus*, USNM 223986, Cavite, Philippines, Feb 13 1916, skull; *Buteo buteo*, S/1952.1.173, Llwyngwair, N. Pembrokeshire, 1916; ♀, USNM 556291, Ede, Holland, 16 Apr 1981; *Hypomorphnus [=Buteogallus] urubitinga*, 1858.5.26.12; *Buteogallus urubitinga urubitinga*, ♂, USNM 319433, Caimancito, Argentina, Jun 1930; *Chelictinia riocourii*, 1904.4.28.3, Gambia; ♀, USNM 569279, Kelam, Ethiopia, 15 Mar 1975, leg bones removed from skin; *Chondrohierax uncinatus uncinatus*, USNM 289784, Santa Marta region, Colombia; Circaetus gallicus, 1930.3.24.261; ♀, USNM 430827, Essex Vale, Southern Rhodesia [Zimbabwe], 15 Sep 1958; *Circus aeruginosus aeruginosus*, 1924.5.31.234, captivity, Apr 1897; ♂, USNM 557495, Kyzyl-Agach, Azerbaijan, USSR, Jan 1977; *Elanoides forficatus*, 1902.2.2.25, Texas; ♂, USNM 289686, Holopaw, Florida, 27 Apr 1925; *Elanus caeruleus*, ♂, 1898.5.7.10, South Africa, 27 Sep 1894; *Elanus caeruleus caeruleus*, ♀, USNM 558447, 23 km north of Capetown, Cape Province, Republic of South Africa, 12 Mar 1981; *Erythrotriorchis radiatus*, 1872.10.22.9, Cape York [Australia]; *Gampsonyx swainsonii*, ♀, USNM 345789, Tres Barras, Brazil, 2 Jul 1941; *Geranoaetus melanoleucos*, ♀, S/1954.10.3, southwest South America, captivity, 6 May 1954; USNM 318388, Cachapol River, Chile; *Geranospiza caerulescens*, 1903.12.20, Serra da Chapada, central Brazil, Jun 1902; *Geranospiza caerulescens nigra*, USNM 18450, Orizaba, Mexico; *Gypaetus barbatus*, 1911.2.9.2; USNM 17834, Algeria, 1842; *Gypohierax angolensis*, 1850.11.13.14; ♂, USNM 291316, Efulan, Cameroun, West Africa, 7 Apr 1927; *Gyps africanus*, S/1983.19.6, Karoi, 16°47′S, 29°35′E, 1983; *Gyps fulvus*, 1861.2.26.6, captivity, 30+ years; *Gyps ruepelli*, ♂, USNM 430014, captivity, 2 Feb 1958; *Haliaeetus albicilla*, 1851.11.10.46?; *Haliaeetus leucocephalus*, 1930.3.24.262, May 1911; ♂, USNM 431884, Yakutat, Alaska, Jan 1961; *Haliastur indicus*, USNM 556985, Jailolo District, Halmahera Is, Moluccas, Indonesia, 2 Apr 1981; *Haliastur sphenurus*, S/1964.1.14, Harrow, Victoria, Australia, 24 Jan 1963; *Harpagornis moorei*, ♀?, NMNZ S 27773, Mount Owen, Nelson, New Zealand, Jan 1990; *Harpagus dentatus*, USNM 559320, 10 miles up Cuyuni River, Guyana, 8 Jan 1984; *Harpia harpyja*, 1872.10.25.1; ♀, USNM 429223, captivity, Nov 2 1949; ♀, USNM 429223, captivity, 2 Nov 1949; *Harpyhaliaetus solitarius*, USNM 49656, San Geronimo, Guatemala, 2 leg bones ex skin same number; *Heterospizias meridionalis*, ♀, 1903.12.20.1, Serra da Chapada, central Brazil;

Heterospizias meridionalis meridionalis, USNM 227378, Puerto Pinasco, Paraguay, 8 Sep 1920; *Hieraaetus fasciatus*, 1847.10.21.50; *Hieraaetus fasciatus spilogaster*, ♂, USNM 430796, Mphoengs, Southern Rhodesia [Zimbabwe], 18 Aug 1958; *Ichthyophaga ichthyaetus*, 1845.1.12.20; USNM 468555, captivity, 7 Jan 1958; *Ichthyophaga humilis [=nana]*, ♂, USNM 224807, Toli Toli, Celebes [Sulawesi], Indonesia, 8 Dec 1914; *Ictinaetus malayensis*, ♀, S/1969.1.1, Gunong Benom, Malaya; *Ictinia plumbea*, ♂, 1903.12.20.253, Serra da Chapada, Brazil, 29 Oct 1902; *Kaupifalco monogrammicus*, ♂, 1869.10.19.28, Africa; ♂, USNM 322456, Cameroun, West Africa, 10 Apr 1931; *Leptodon cayenensis*, ♀, USNM 32973, Central America, feet only; *Leucopternis (albicollis?) polionota*, 1846.4.21.18; *Leucopternis melanops*, ♀, USNM 432181, captivity, 23 Jul 1963; *Lophaetus occipitalis*, 1861.1.19.6; ♂, USNM 291451, Temkaka, Sudan, Africa, 28 Feb 1928; *Machaerhamphus alcinus*, ♀, adult, S/1956.20.1, Gomantong, North Borneo, 16 Apr 1956; USNM 559816, Gomantong Caves, 35 km south of Sandakan, Sabah, Malaysia, Dec 1982; *Melierax musicus* (*M. canorus*), 1903.1.6.13, Deelfontein; *Melierax gabar*, ♂, USNM 290384, Africa, Oct 28 1926; *Milvus milvus milvus*, ♂, 1940.7.6.1, Wales; *Milvus migrans lineatus*, ♀, USNM 319228, Szechwan, China, 21 Jul 1930; *Morphnus guianensis*, 1851.12.2.10; ♂, USNM 432243, captivity, 4 Aug 1963, trunk skeleton; USNM 18468, skull; *Necrosyrtes monachus*, 1860.1.19.8, Natal; USNM 18894, Cunga, Angola, West Africa; *Neophron percnopterus*, 1847.10.21.25, South Africa; USNM 17835, North Africa; *Parabuteo unicinctus harrisi*, ♀, 1900.11.30.30, Brownsville, Texas, 6 May 1900; ♂, USNM 343414, Starr County, Texas, Jul 25 1936; *Pernis apivorus*, 1871.12.29.3; *Pernis apivorus gurneyi*, USNM 343983; Chiengmai, northern Siam [Thailand], 20 Jan 1937; *Pithecophaga jefferyi*, S/1961.23.1, captivity, Nov 1961; ♂, captivity, 30 Jun 1970; *Polyboroides radiatus*, 1860.12.31.1, Natal; *Polyboroides typus*, ♀, USNM 291787, Efulan, Cameroun, West Africa, 4 Feb 1928; *Polemaetus bellicosus*, S/1957.9.1, Africa, captivity, 20 May 1957; ♂, USNM 430533, Syringa, Southern Rhodesia [Zimbabwe], 30 Nov 1957; *Rostrhamus sociabilis*, ♂, USNM 553612, Buenos Aires, Argentina, 4 Mar 1966, captivity; *Spilornis cheela bassus*, 1850.8.15.14, India; *Spilornis cheela*, 1845.1.12.12, Nepal; *Spilornis cheela burmanicus*, ♂, USNM 343985, San Sai Luang (near Chiengmai), northern Siam [Thailand], 27 Feb 1936; *Spizaetus ornatus*, S/1952.1.177; ♂, USNM 430495, captivity, 15 Mar 1958; *Spizastur melanoleucos*, USNM 321507, Velhas River, Brazil, 1866; *Stephanoaetus coronatus*, ♀, S/1954.30.42; ♂, USNM 346652, captivity, 15 May 1943; *Terathopius ecaudatus*, 1853.1.21.2, South Africa; ♂, USNM 431431, Norton, Southern Rhodesia [Zimbabwe], 3 Jul 1961; *Urotriorchis macrourus batesi*, ♂, USNM 292398, Efulan, Cameroun, West Africa, Aug 6 1928.

Several taxa were represented in collections only by part skeletons, or a few bones removed from study skins. Material of others (*Dryotriorchis, Megatriorchis, Harpyopsis, Eutriorchis, Oroaetus, Hamirostra, Lophoictinia, Henicopernis*) was either not available in the collections visited, or was not held in collections at the time (Blandamer & Burton 1979; Schnell & Woods 1984).

Sarcogyps and *Torgos* are sometimes recognised as monotypic genera, but were included in *Aegypius* by Amadon (1977) and Stresemann & Amadon (1979). Only *Aegypius* was examined in this study.

South-east Asian species of *Spizaetus* were poorly represented in collections, so that genus, as presently understood (Stresemann & Amadon 1979), was represented by the American *Spizaetus ornatus*. The absence of south-east Asian taxa is unfortunate, because they are geographically one of the closest groups of forest eagles to *Harpagornis moorei*, and have been suggested as possibly their closest relatives (Brathwaite 1986).

5.2.2 Analysis of characters

I used only qualitative, multi-state osteological characters so that *Harpagornis moorei* could be scored for all characters used in the analysis. Most characters were defined after examination of series of homologous elements from as full a range of taxa as possible. Other characters had already been defined or illustrated, primarily by Jollie (1976, 1977a, 1977b, 1977c) and Olson (1982, 1987).

Of 273 characters assessed, 188 were used in the analysis of 45 taxa, including the outgroup (mean 4.2 features per OTU). The other characters either could not be assessed for sufficient taxa, or their different states could not be surveyed properly in the time I had available with collections. I nevertheless describe the unused characters so they can be considered in future work.

All skeletal characters were discrete features having at least two definable states. Character states were tabulated for each OTU. Characters were assumed to be homologous if they involved similar structures in corresponding positions on the same elements. Most could be described using standard terminology (Ballmann 1969; Baumel 1979; Howard 1929), and are therefore subject to the least possible error in assumed homology as present knowledge of avian osteology permits. Most difficulty was experienced in reconciling characters of *Sagittarius* and *Pandion* with those in similar anatomical positions in accipitrids.

Whenever possible, characters were checked for intraspecific and interspecific variation; where this was found, the feature was reassessed or omitted if the variation was considered to be too great.

Characters were weighted equally because there was no reliable information on the conservativeness of any particular feature. Characters were coded as missing if no material was available, or if an element was damaged and the state was difficult to determine.

Characters are listed and described in Appendix 5.1, and the OTU-character state matrix is shown in Appendix 5.2. For completeness, the matrix in Appendix 5.3 includes known states of taxa not included in the development of trees presented here.

5.2.3 Trees

I used the program PAUP (Swofford 1985) to generate phylogenetic trees for 42 living genera, *Harpagornis*, *Pandion* and *Sagittarius*. PAUP uses parsimony to produce one or more shortest trees; those in which fewest changes of character state are required. The MULPARS (multiple parsimony) option was invoked, in which all equal length trees are kept until a shorter tree is found. This procedure avoids the possibility that one tree may be accepted from several trees of different topology and the same length. It also helps to reduce the possibility that searching may be limited when rearrangement of a single tree does not result in a shorter tree. If several trees are kept in the computer's memory, it is possible that another equal-length tree will be found from which a shorter tree can be derived (Swofford 1985).

To maximise the chance of finding the shortest tree, the GLOBAL branch swapping option was used. Global swapping involves removing every possible subtree and inserting it at all other positions in search of a shorter tree.

The Accipitridae is apparently so isolated phylogenetically that it is difficult to determine the higher taxon with which it shares its most recent common ancestor (Olson 1985). In alternative recent classifications, *Sagittarius* is considered to be a subclade of either the major clade Order Falconiformes (Stresemann & Amadon 1979) or the Parvorder Accipitrida (Sibley & Ahlquist

1988). I did not use the Falconidae as an outgroup because it was more difficult to assess the homology of characters between the Accipitridae and Falconidae than between the accipitrids and *Sagittarius*. The outgroup was chosen from within the small group of postulated closest relatives, because it was not an object of this study to investigate the relationships of the accipitrids with other families.

Polarities of character state changes were not assumed, and I did not attempt to derive transformation series for the character states. With the data unordered option in effect, PAUP algorithms develop transformation series for the features, and do not assume that transformation series were known. Primitive and derived states were generated by PAUP by outgroup comparison, using *Sagittarius* as the outgroup. This was done because of the limited aims and exploratory nature of the study, and the short time available for examination of the full range of material. Examination of the characters used suggests that it should be possible to derive transformation series for them on outgroup and ontological criteria when a full analysis of the Accipitridae is undertaken. Transformation series generated by PAUP were assumed to be linear.

Pandion was tried as the outgroup, and the trees produced were similar, but not identical in topology to those produced using *Sagittarius*. *Sagittarius* was the preferred outgroup because its separation from the Accipitridae is supported by a range of evidence (de Boer & Sinoo 1984; Jollie 1976, 1977a, 1977b, 1977c). On the other hand, there is some support for the hypothesis that *Pandion* and the accipitrids share a most recent common ancestor (Sibley & Ahlquist 1972; Tyler 1966).

No ontogenetic information was available for most characters used and as a consequence developmental data could not be used to determine character state polarities. I did not use the criterion of wide representation of a character indicating plesiomorphy (primitiveness), because of the apparent homogeneity of morphology and the high level of plesiomorphy within the family suggested by karyological data (de Boer & Sinoo 1984).

All taxa compared were taken as belonging to a single, natural clade because all species in the family that have been studied so far share the derived

condition, apparently unique within Aves, of having only 6-12 microchromosomes (de Boer & Sinoo 1984).

5.2.4 Comparisons with other data

Trees were assessed by making comparisons with published classifications, and with morphological and other data available in the literature. Trees were also compared with information on host-parasite relationships of bird lice (Mallophaga) and results of a biogeographic analysis (see below). It was not possible to use data from fossils (Olson 1985), but the presence of Vulturidae in Europe during the Tertiary (Cracraft & Rich 1972), and of accipitrid vultures in North America until the late Pleistocene (Rich 1980), were taken into account.

5.2.5 Biogeography of the Accipitridae

Patterns of distribution of living accipitrids were analysed by using genera as characters, and numbers of species in each genus as character states. This is a modification of the method discussed by Brooks (1985). OTUs were geographic regions that usually coincided with boundaries and sub-boundaries of biogeographic regions. Numbers of species in each genus in each of 18 areas were compiled from distributional data and maps provided by Brown & Amadon (1968) and Stresemann & Amadon (1979).

Trees were produced using PAUP (Swofford 1985), with MULPARS and GLOBAL branch swapping options selected, and character states unordered. The tree topologies were then compared with those obtained from the phylogenetic study.

5.3 RESULTS

5.3.1 General

Two shortest trees were found with almost identical topologies (consistency index 0.217). They differed only in the position of *Gypaetus* in the accipitrid vulture clade (see below). The main branches of the second tree are shown in Fig. 5.1. Details of the branches are shown in Fig. 5.2-5.13.

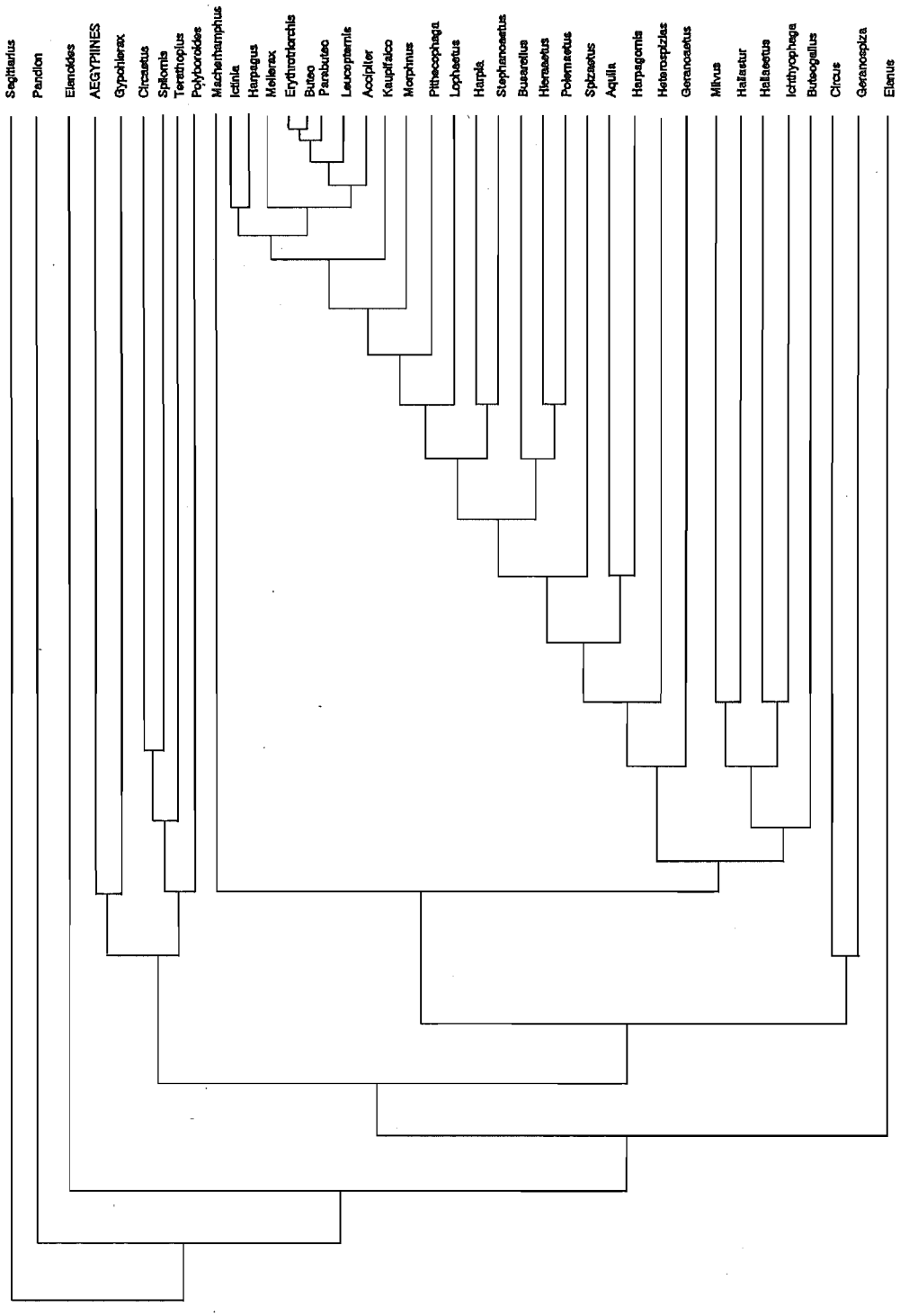

Fig. 5.1 Phylogenetic tree of the Accipitridae derived from analysis of 188 osteological characters. Aegypiines are resolved in Fig. 5.4 and 5.5. See Table 5.1 for taxa representing each genus. See Appendix 5.1 for characters.

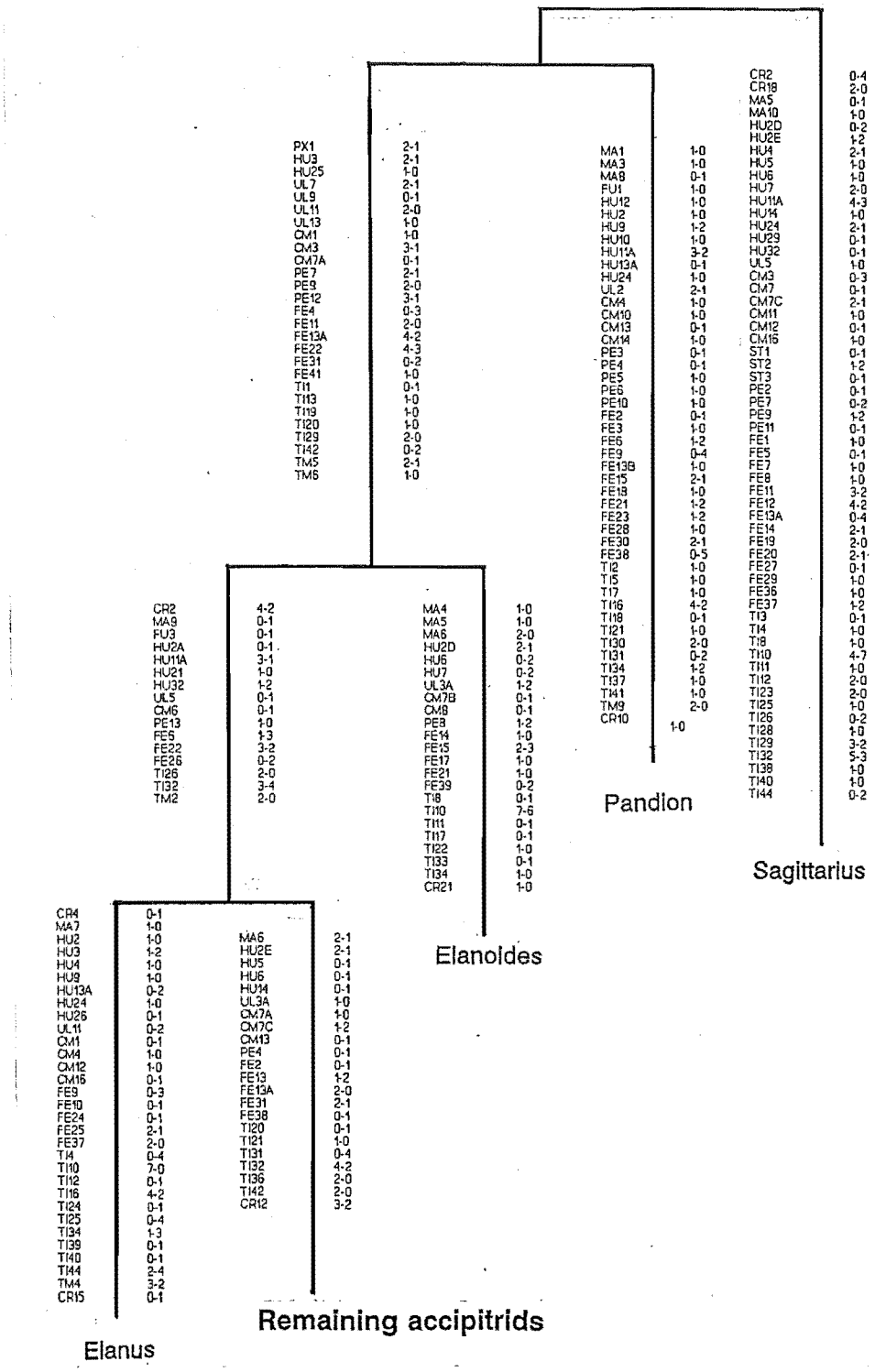

Fig. 5.2 Basal branches of phylogenetic tree of the Accipitridae, including the outgroup (*Sagittarius*), and *Pandion*. The 'kites' *Elanoides* and *Elanus* are symplesiomorphically similar. Character state changes shown on each branch: see Appendix 5.1 for descriptions of characters.

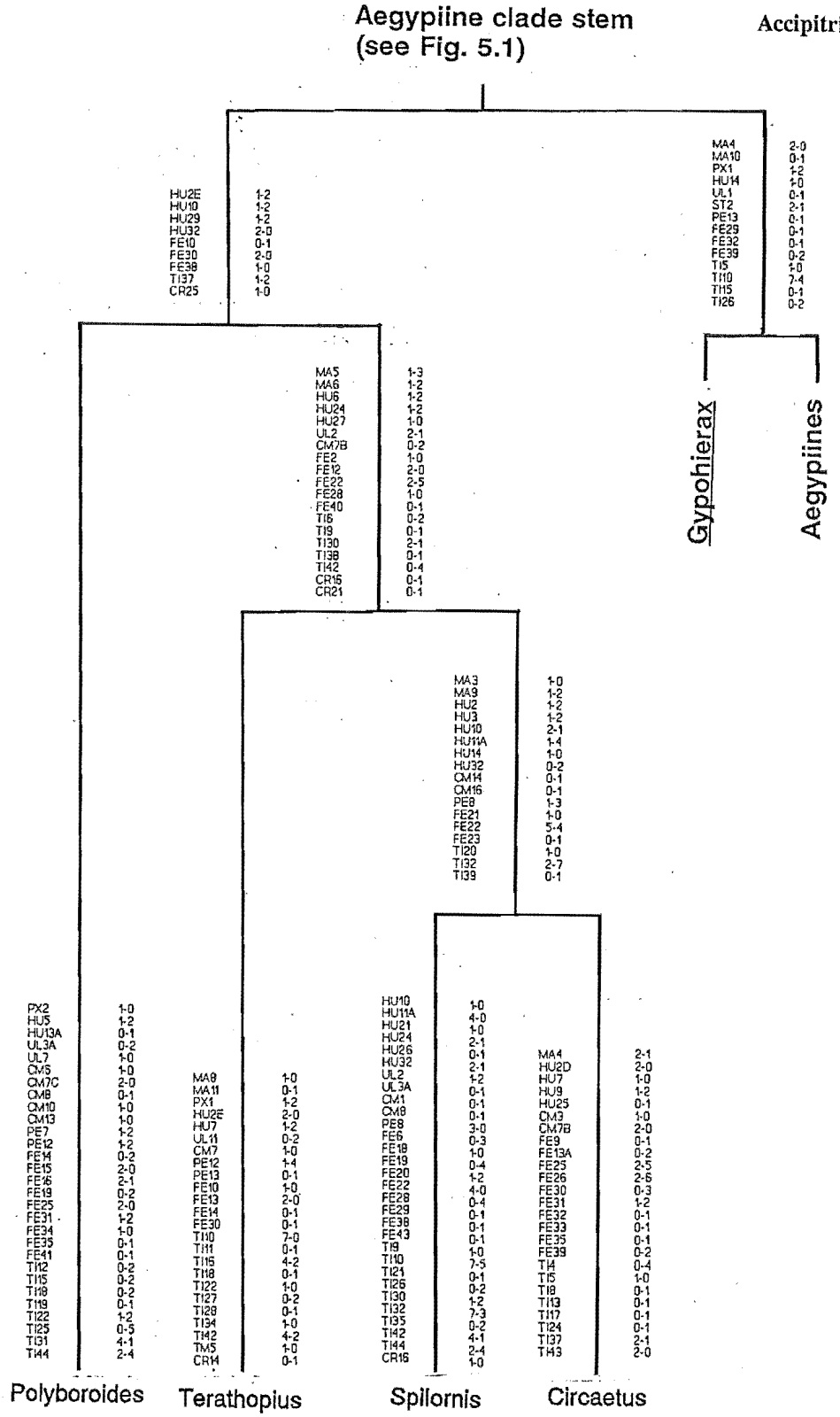

Fig. 5.3 'Serpent' and 'snake' eagles (*Spilornis* and *Circaetus*, the African Harrier-Hawk (*Polyboroides*), and the Bateleur (*Terathopius*). Basal branches of the vulturine clade of the phylogenetic tree of the Accipitridae. See Fig. 5.4 and 5.5 for further branches. For stem branch, see Fig. 5.1. Character state changes shown on each branch: see Appendix 5.1 for descriptions of characters.

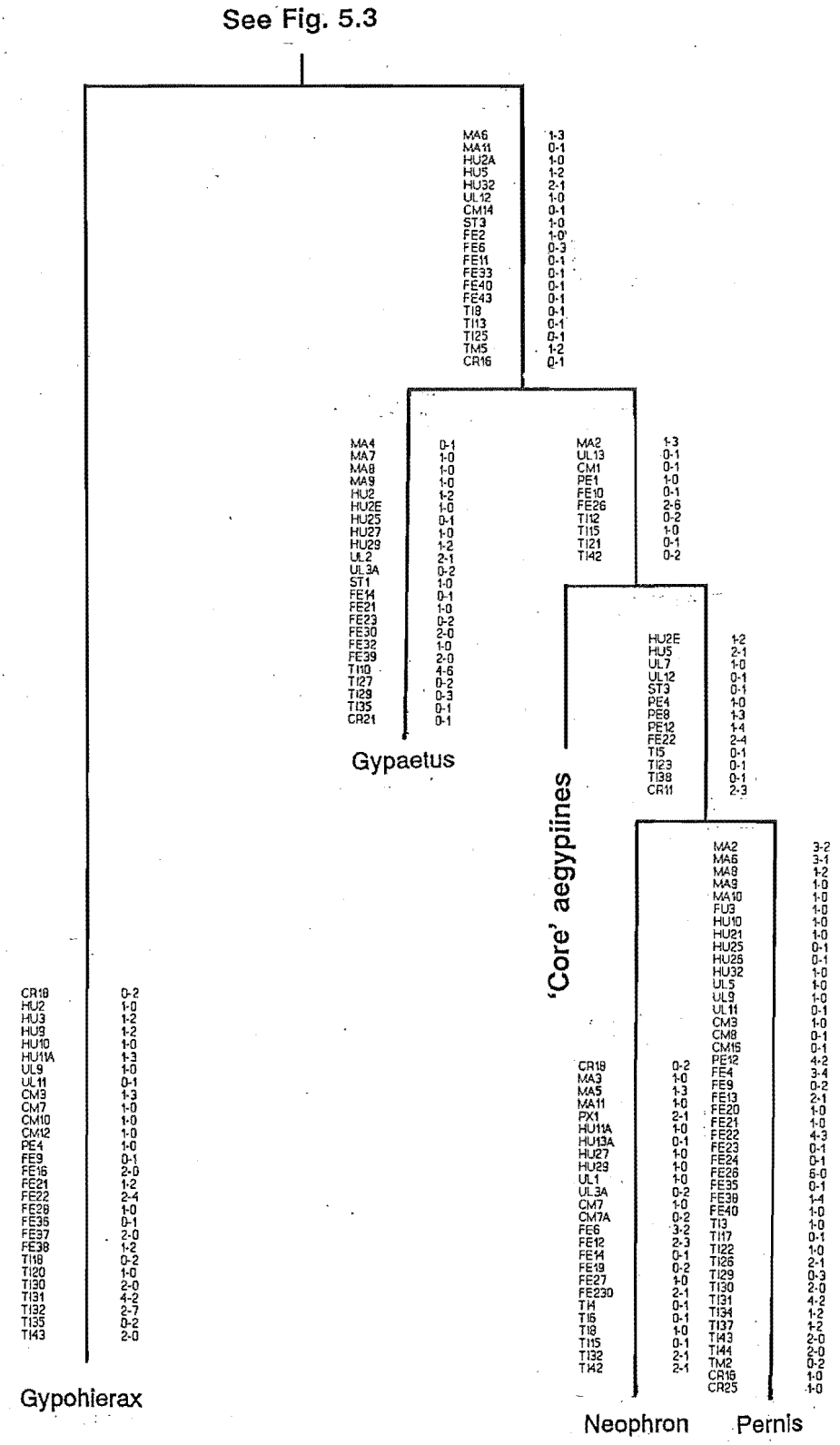

Fig. 5.4 Large vulturines, including the 'Palm-nut Vulture' (*Gypohierax*), the Bearded Vulture (*Gypaetus*), the Egyptian Vulture (*Neophron*), and the Honey Buzzard (*Pernis*). Character state changes shown on each branch: see Appendix 5.1 for descriptions of characters.

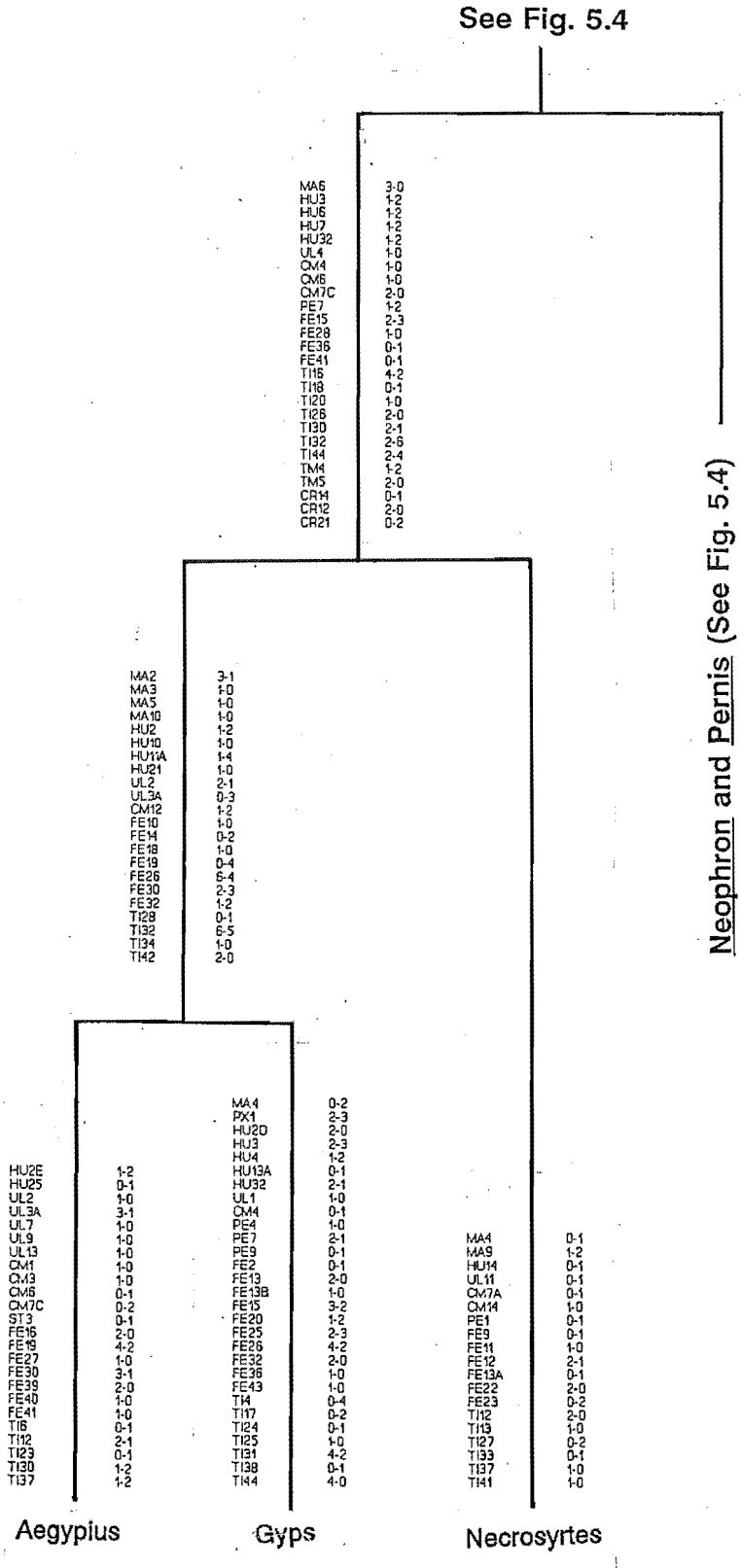

Fig. 5.5 Large vultures. Black (*Aegypius*) and Griffon (*Gyps*) vultures, and Hooded Vulture (*Necrosyrtes*). Character state changes shown on each branch: see Appendix 5.1 for descriptions of characters.

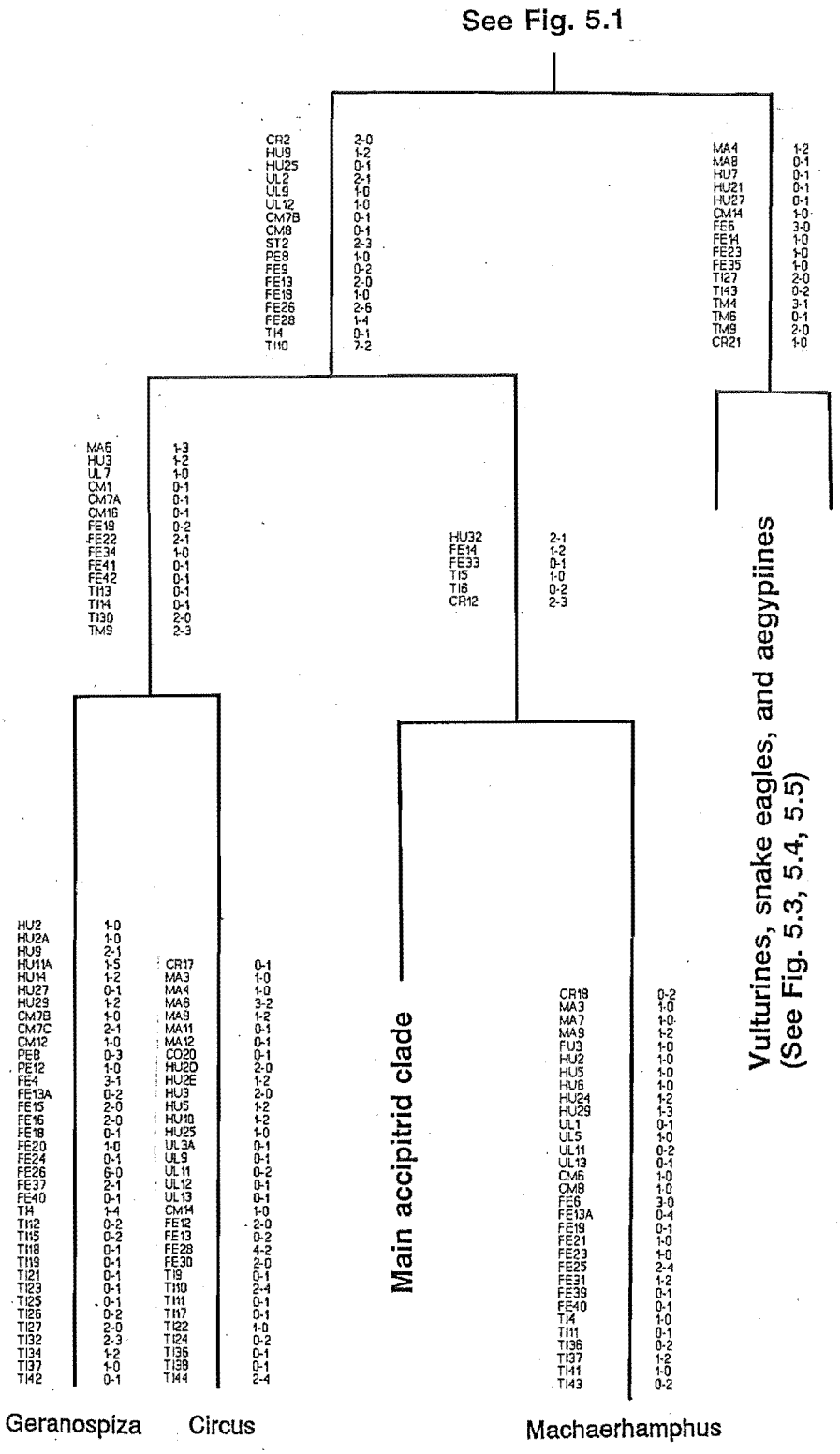

Fig. 5.6 Basal branches of the main accipitrid clade, showing two 'minor' clades, the harriers (*Geranospiza* and *Circus*) and the Bat Hawk (*Machaerhamphus*) relative to the aegypiine clade, and the 'core' or 'typical' accipitrids (for which see Fig. 5.7-5.13). Character state changes shown on each branch: see Appendix 5.1 for descriptions of characters.

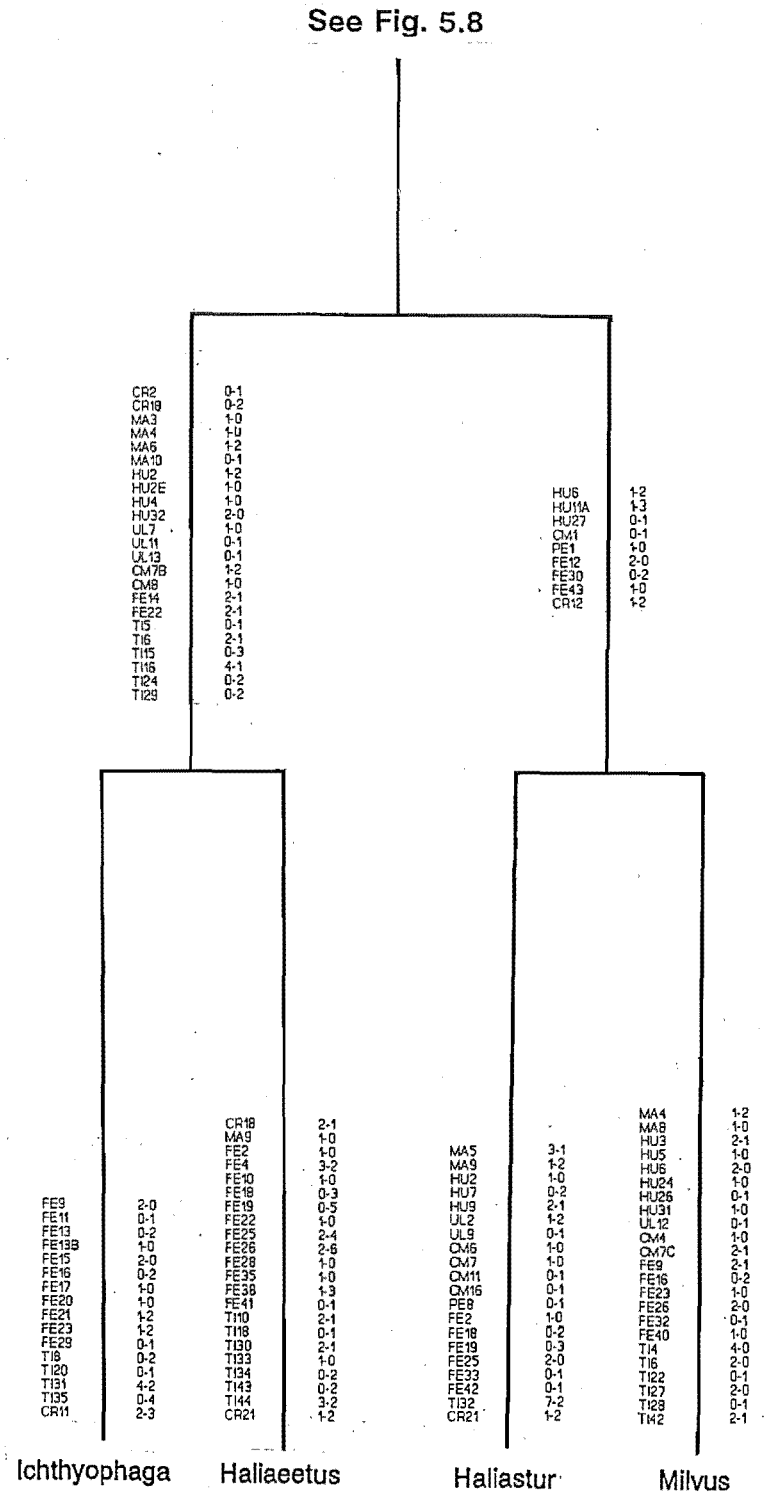

Fig. 5.7 The 'fish eagle' (*Ichthyophaga* and *Haliaeetus*) and 'milvine kite' (*Haliastur* and *Milvus*) clade, showing the sister-group relationships. See Fig. 5.8 for relationship to *Buteogallus* and 'core' taxa. Character state changes shown on each branch: see Appendix 5.1 for descriptions of characters.

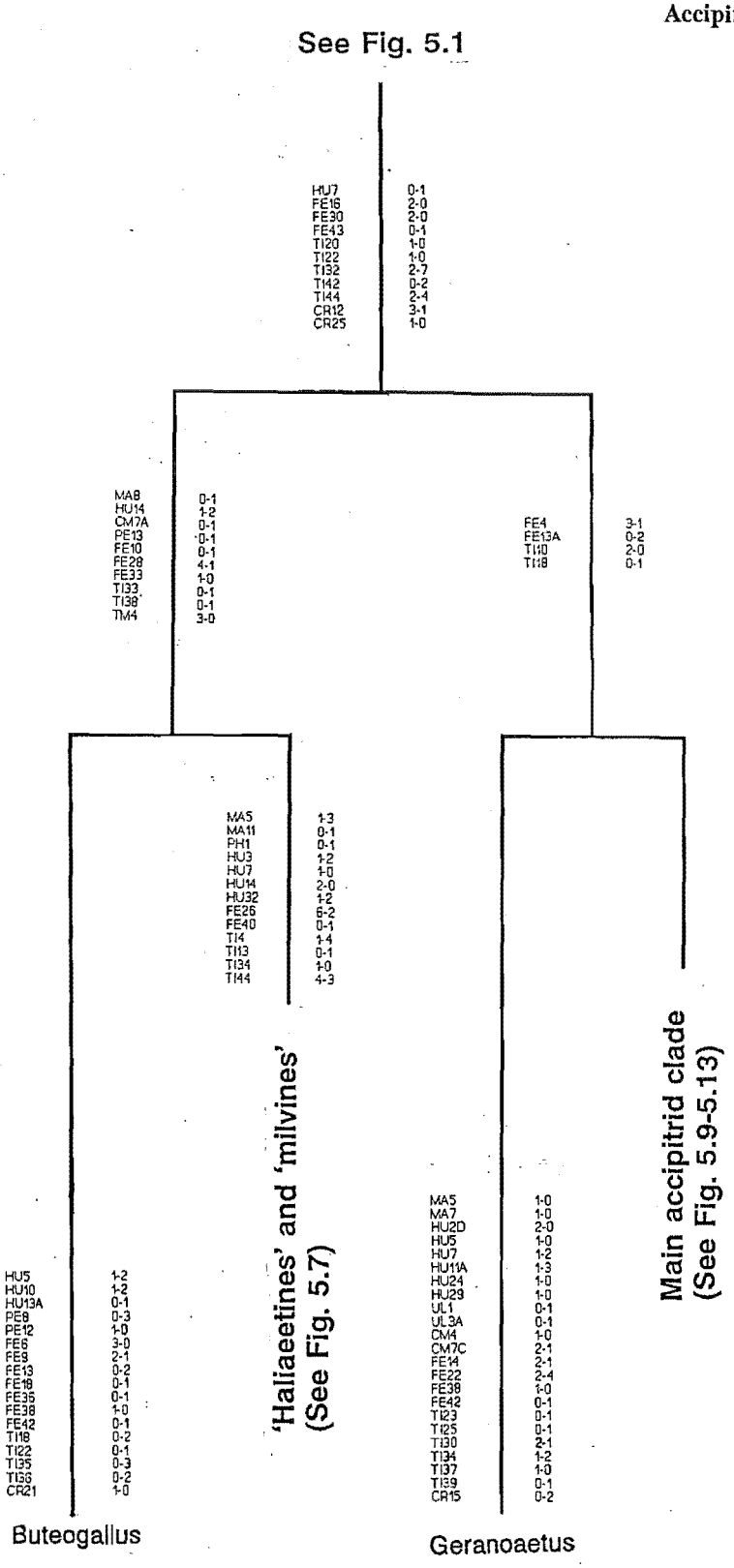

Fig. 5.8 Relationship of Black Hawk (*Buteogallus*) and Buzzard Eagle (*Geranoaetus*) to milvine-haliaeetine clade, and to 'core' taxa. Character state changes shown on each branch: see Appendix 5.1 for descriptions of characters.

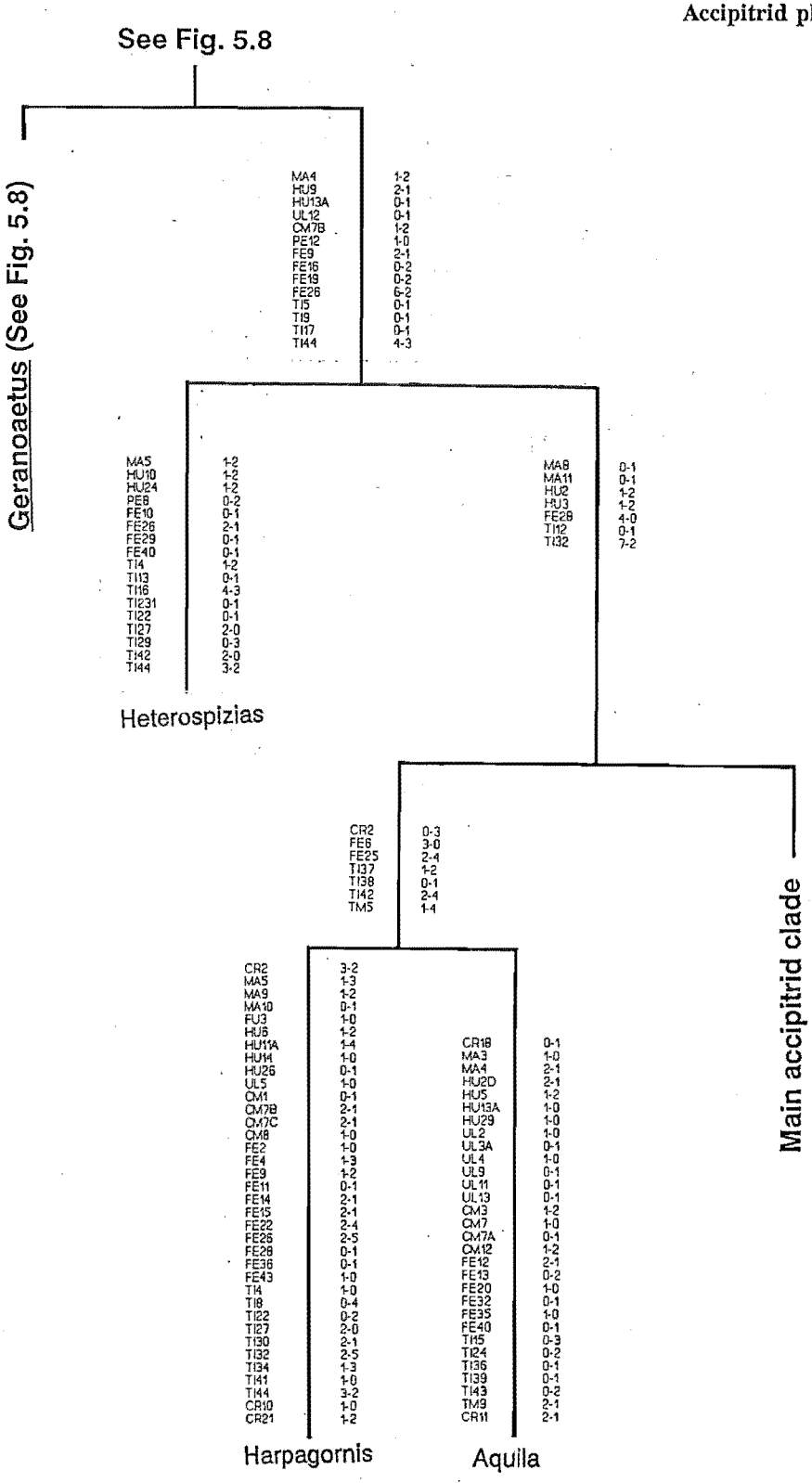

Fig. 5.9 Relationship of the Savannah Hawk (*Heterospizias*) to the aquilines and 'core' taxa; and the sister-group relationship of Haast's Eagle (*Harpagornis*) and the golden eagles (*Aquila*). Character state changes shown on each branch: see Appendix 5.1 for descriptions of characters.

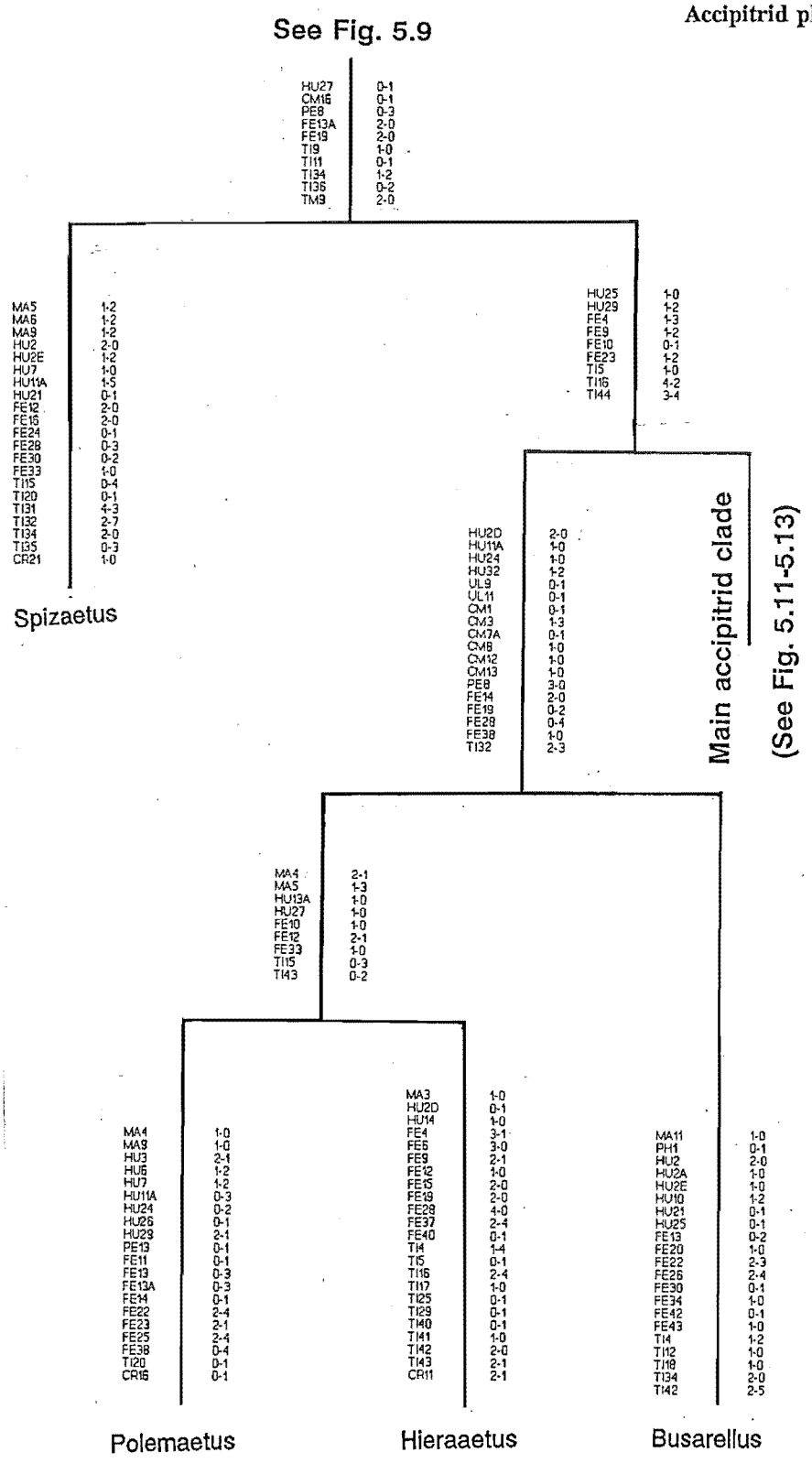

Fig. 5.10 Relationship of the 'hawk eagles' of the genera *Spizaetus* and *Hieraaetus*. The African Martial Eagle (*Polemaetus*) is a sister-group of *Hieraaetus*, and the Black-collared, or Fishing, Hawk (*Busarellus*) is a sister-group of the Old World hawk eagles. Character state changes shown on each branch: see Appendix 5.1 for descriptions of characters.

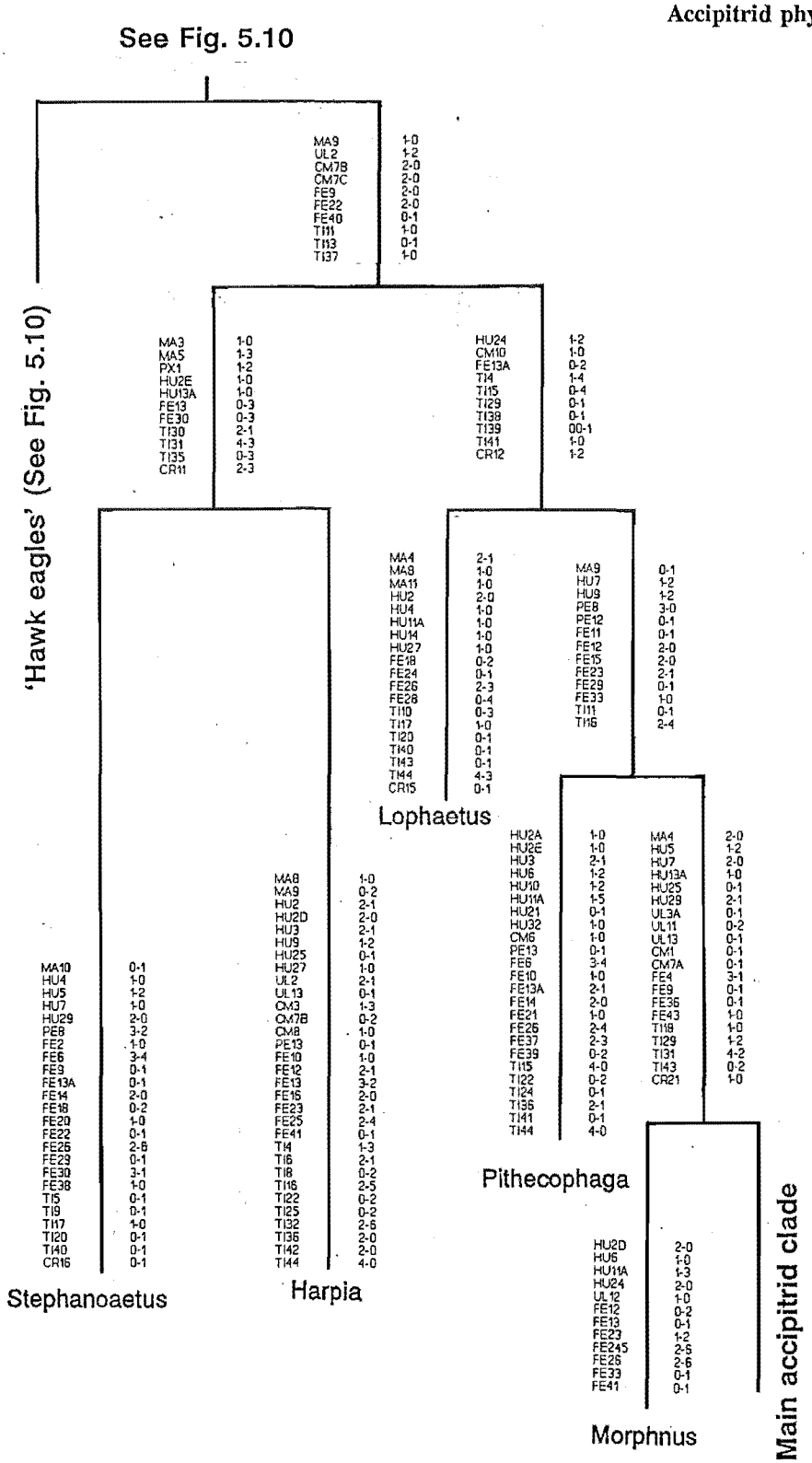

Fig. 5.11 The 'Harpy' eagles, showing the sister-group relationship of the African Crowned Eagle (*Stephanoaetus*) and the South American Harpy (*Harpia*), but the paraphyly of the other great forest eagles. In particular, the Guianan Crested Eagle (*Morphnus*) is sister-group to the accipitrid 'core' taxa (see Fig. 5.12, 5.13). Character state changes shown on each branch: see Appendix 5.1 for descriptions of characters.

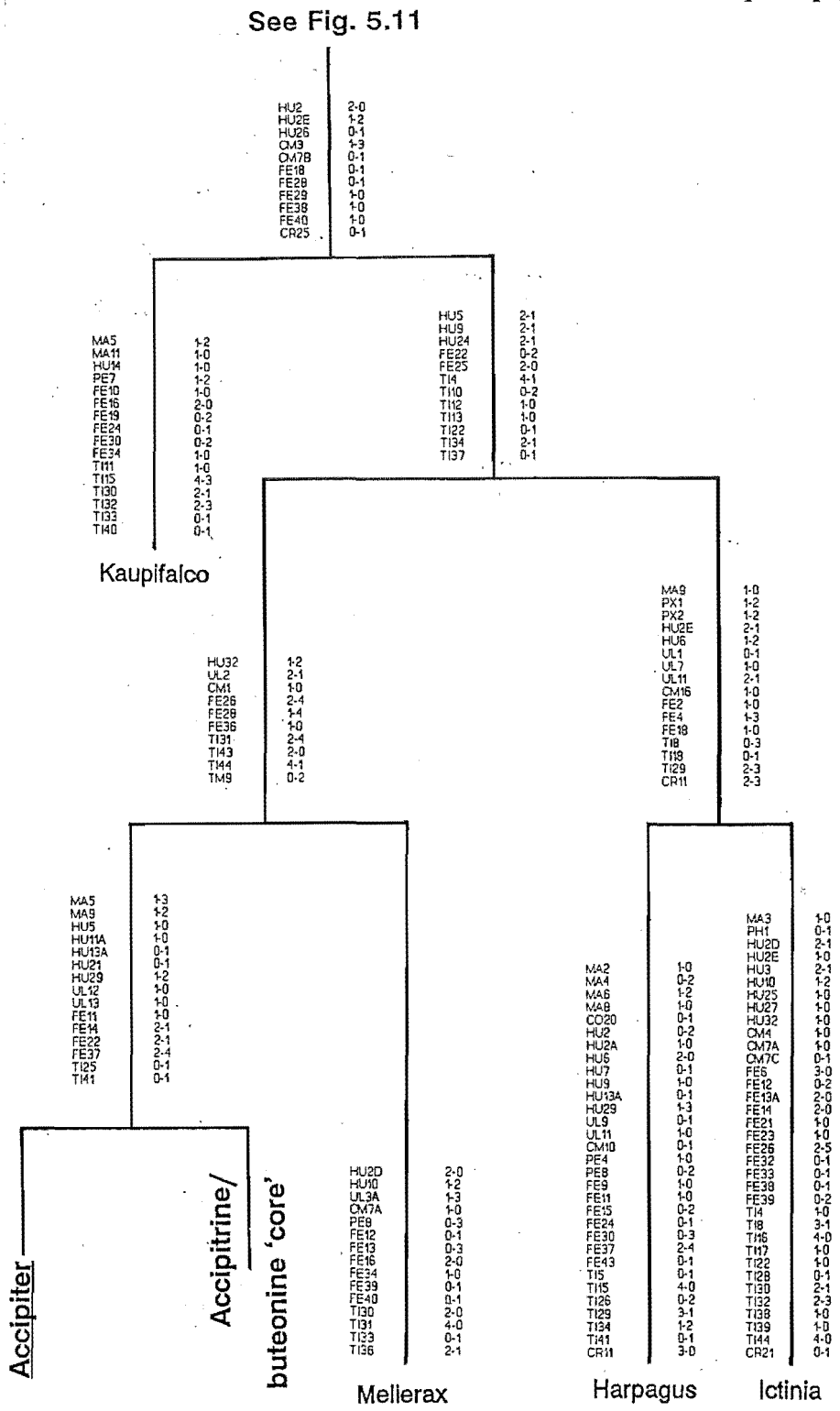

Fig. 5.12 Basal branches of the accipitrid 'core'. The Tooth-billed Kite (*Harpagus*) and Mississippi Kite (*Ictinia*) are accipitrids near *Accipiter* and *Buteo* and not 'elanids'. Character state changes shown on each branch: see Appendix 5.1 for descriptions of characters.

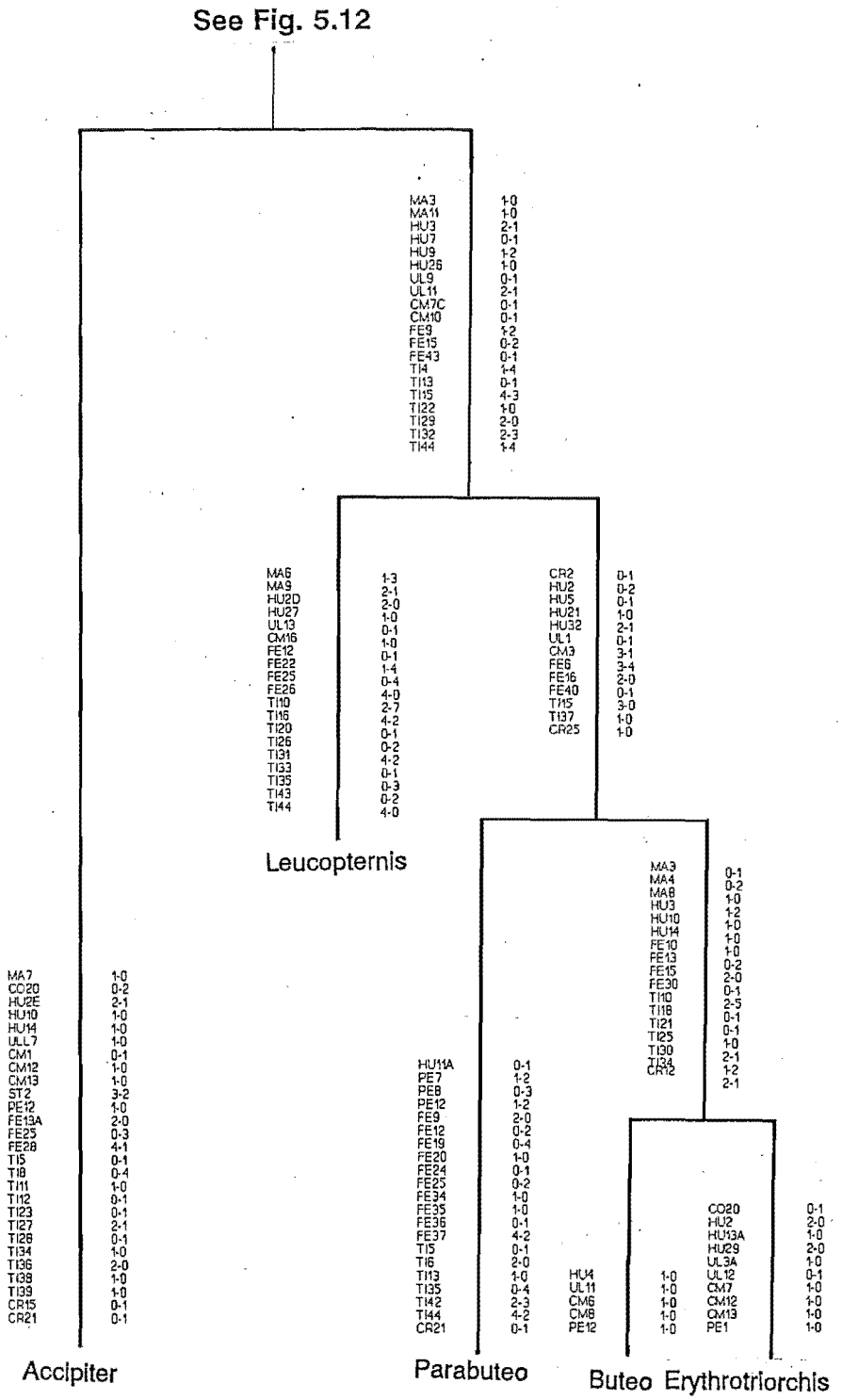

Fig. 5.13 The accipitrid 'core', comprising the 'sub-buteos' (White Hawk, *Leucopternis*, and Harris's Hawk, *Parabuteo*) and the goshawks and sparrowhawks (*Accipiter*) and buzzards (Buteo). *Accipiter* is the sister-group of the other taxa. The Australian Red 'Goshawk' is sister-group to *Buteo*. Character state changes shown on each branch: see Appendix 5.1 for descriptions of characters.

The results confirmed the monophyly of several groups that have been recognised at various taxonomic levels in different classifications.

5.3.2 Basal branches

Sagittarius was separated from the other taxa by 59 characters, including 11 unambiguous autapomorphies. My results supported karyological evidence that *Sagittarius* is not close to the Accipitridae (de Boer 1976).

Pandion branched off first in the main sequence, and was almost as far from the accipitrids as was the outgroup (*Sagittarius*). Forty-six characters, including 13 autapomorphies, supported its distinction. Ten characters were unique to *Pandion* (Fig. 5.2). The separation of *Pandion* from the Accipitridae agreed with conclusions based on pterylosis (Compton 1938), karyology (Ryttman *et al.* 1987), and osteology (Jollie 1976, 1977a, 1977b, 1977c), but some degree of relationship is indicated by eggshell structure (Tyler 1966).

My results confirmed the polyphyly of the 'kites' *sensu* Brown & Amadon (1968). *Elanus* and *Elanoides* were separate clades (Fig. 5.1, 5.2). *Elanoides* was defined by 23 characters, but no autapomorphies. *Elanus*, however, had five autapomorphies among 31 characters. Osteological characters confirmed the separation of these genera; Friedmann (1950) and Brown & Amadon (1968) also separated them on claw morphology.

I had insufficient data to test whether *Gampsonyx* and *Chelictinia* are sister groups of *Elanus* as is implied by Friedmann's (1950) grouping of the three genera in the subfamily Elaninae.

5.3.3 Accipitrid vultures and the serpent eagles

Monophyly of the accipitrid vultures and the so-called 'serpent eagles' was supported by 17 characters, including two autapomorphies within the Accipitridae as accepted here (one was shared with *Pandion*, Fig. 5.2).

The clade included two major branches, with 14 characters defining the vultures, and nine the serpent eagles (Fig. 5.3, 5.4, 5.5). The vultures (Fig. 5.4, 5.5) included three genera (*Gypaetus, Neophron*, and *Gypohierax*), whose proximity to the typical vultures has been questioned (Brown & Amadon 1968;

Jollie 1977c), and one (*Pernis*) which has usually been included with the elanoidid kites (Jollie 1977c). The serpent eagle branch included *Polyboroides* (African Harrier-Hawk) and *Terathopius* (Bateleur Eagle), in addition to *Spilornis* (Asiatic serpent eagles) and *Circaetus* (Snake Eagles of Eurasia and Africa).

Inclusion of *Polyboroides* with the serpent eagles was based on 29 characters (Fig. 5.3). Three of 17 convergences were with *Geranospiza* (South American Crane Hawk), whose relationship to *Polyboroides* has been debated for many years (Burton 1978; Brown & Amadon 1968; Friedmann 1950; Jollie 1977c).

Friedmann (1950) thought that they were closely related, whereas Brown & Amadon (1968: 21) stated that *Polyboroides* is "definitely related to the snake-eagles and might be regarded as only a specialised member of that group". They based this view partly on the similarity of the plumage of the young to that of *Spilornis*. Burton (1978) concluded that the shared derived characters of the intertarsal joint seemed to support a relationship but could not exclude the possibility of convergence of these characters. He noted, however, that if the intertarsal joint criterion was omitted, then there was little evidence for a close relationship between the two taxa. Jollie (1977c) placed *Polyboroides* with the accipitrid vultures and serpent eagles, and *Geranospiza* grouped them with South American '*sub*-Buteos'. Pycraft (1889) noted that *Polyboroides* was similar in its myology to *Gypohierax*.

My data confirmed a relationship between *Polyboroides* and the serpent eagles, but as a plesiomorphic taxon within the group rather than a highly specialised (derived) one as suggested by Brown & Amadon (1968). Nevertheless, it did exhibit four autapomorphies.

Terathopius did not possess any autapomorphies, but was defined by a suite of 24 characters, including 17 convergences 6 reversals, and one complex character. The inclusion of *Terathopius* with the serpent eagles supports Brown & Amadon's (1968) interpretation. Jollie (1977c) concluded that it was intermediate between the serpent eagles and the accipitrid vultures.

The clade of serpent eagles was defined by 17 characters (Fig. 5.3). *Spilornis* lacked an autapomorphy among a suite of 30 distinguishing characters. *Circaetus*, however, had one autapomorphic character among the 25 that separated it from *Spilornis*. Brown & Amadon (1968) and Jollie (1977c) considered the two genera were closely related.

de Boer & Sinoo (1984) found that *Circaetus gallicus* had a karyotype identical to that of the accipitrid vultures, and only slightly different from that of *Pernis*. The karyological data provide some support for the branching pattern found here.

In the vulturine branch, the separation of *Gypohierax* (Palmnut vulture) was supported by 28 characters, but no autapomorphies (Fig. 5.4). *Gypohierax* was included with the vultures by Brown & Amadon (1968), who suggested that it linked them to the sea eagles (*Haliaeetus*). Brown & Amadon (1968) also suggested that it most resembled *Neophron* (Egyptian vulture) amongst the other vultures, a view also held by Jollie (1977c) and Suschkin (1899), but not confirmed here.

The monophyly of a group consisting of *Pernis* (honey buzzards) and *Neophron* was supported by 13 characters, but none of these was an unambiguous autapomorphy (Fig. 5.4). As noted above, *Pernis* has usually been placed near *Elanoides* (Brown & Amadon 1968; Jollie 1977c) and not with the accipitrid vultures. However, Brown & Amadon (1968) implied that there was at least a distant relationship by suggesting that the vultures had evolved from kites, and Jollie (1977c) noted that *Neophron* is "'kite-like' in many respects", although it superficially resembles *Necrosyrtes*. *Pernis* was characterised by four autapomorphies, and *Neophron* by three and another character shared with *Pandion* (Fig. 5.4).

The position of the bearded vulture, *Gypaetus*, in the branching sequence of the accipitrid vultures was the only difference between the two shortest trees. In the first tree, *Gypaetus* was the sister group of a clade containing *Necrosyrtes* (African hooded vulture), *Gyps* (griffon vultures), and *Aegypius* (black and lappet-faced vultures of Africa and Eurasia) (Fig. 5.5). In the second tree (Fig. 5.4), *Gypaetus* was the sister group of all the vultures except *Gypohierax*.

de Boer (1976) concluded that the differences between the karyotypes of *Gypaetus* and the other vultures did not support a close relationship between the former and the vultures, and more recently de Boer & Sinoo (1984) also rejected the relationship. Instead, they proposed that *Gypaetus* was near *Circus* (harriers), *Pernis*, and the so-called booted eagles (including *Aquila* and *Spizaetus* (de Boer & Sinoo 1984). However, they also noted that the condition in *Gypaetus*, *Pernis*, and the booted eagles could have evolved independently from an 'original' condition, namely that found in *Circaetus*. Such thinking is more in line with my second tree than my first.

Clay (1951) proposed that the Accipitridae and the Vulturidae constitute a monophyletic group because they share the same taxa of bird lice (Mallophaga). However, at that timer it was not clear that accipitrid ('Old World') and vulturid ('New World') vultures had been sympatric in Europe and North America for millions of years, and until as recently as the late Pleistocene in North America (Cracraft & Rich 1972; Howard 1932; Olson 1985; Rich 1980). Clearly, there was ample time for lice to have colonised new hosts, particularly when both host groups probably fed at the same carcases, and their presence on both cannot be considered indicative of a close relationship between the hosts.

Monophyly of the remaining three genera (*Necrosyrtes, Gyps*, and *Aegypius* was supported by 26 characters (19 convergences, 6 reversals, 1 synapomorphy) (Fig. 5.5). *Gyps* and *Aegypius* were linked by a single synapomorphy which was immediately reversed in *Gyps*; 21 other characters supported their monophyly. *Gyps* was characterised by three autapomorphies. Jollie (1977c) recognised a similar grouping of these three genera, as did Brown & Amadon (1968).

5.3.4 *Circus* and *Geranospiza*

Circus was found to be the sister group of *Geranospiza* (Fig. 5.6), and not a sub-buteonine (Amadon 1982b). Nor was it close to *Accipiter* as suggested by Jollie (1977c), despite the apparent close resemblance of its postcranial anatomy (Olson & James 1991). The monophyly of the clade consisting of *Geranospiza* and *Circus* was supported by two synapomorphies. As noted above, *Geranospiza* was not close to *Polyboroides*. The karyotype of *Geranospiza* (Williams &

Benirschke 1976) differs from the unique *Circus* karyotype (de Boer & Sinoo 1984). This feature supports the likelihood of an early separation of the two genera.

Sibley & Ahlquist (1972) found that the egg white proteins of *Circus* were similar to those of Elanus. The similarity is probably plesiomorphic, because the egg white proteins of these genera were similar to those of *Pandion*.

5.3.5 *Machaerhamphus*

Brown & Amadon (1968) regarded the bat kite *Machaerhamphus* as an aberrant elanoidid kite. However, Jollie concluded that the skeletal evidence was equivocal and suggested that it is "an extreme type without close relatives ... [that had] ... a long and independent history" (Jollie 1977c: 121(321)).

My phylogenetic reconstruction indicated that it represented a separate clade, whose monophyly was supported by two autapomorphies, one of which was, however, shared with the outgroups (Fig. 5.1). It was linked to other 'kites' only by symplesiomorphies.

5.3.6 Milvine kites and sea eagles

The data support a sister group relationship between the milvine 'kites' (*Milvus* and *Haliastur*) and the sea and fishing eagles (*Haliaeetus* and *Ichthyophaga*) (Fig. 5.7). However, *Buteogallus* (the South American black hawks) was an unexpected member of the clade. Jollie (1977c) placed it with *Heterospizias* and *Busarellus* in the same clade as the Harpies, whereas Brown & Amadon (1968) included it with *Heterospizias* and *Leucopternis*. Jollie (1977c: 117-118) grouped *Buteogallus* with *Heterospizias* and summed up the problems of relationships among the Accipitridae when he pointed out that "the Central and South American species of the buteogallin supergenus appear to retain more of the primitive features, a statement that is more of a hope than a defensible hypothesis".

Monophyly of the whole clade was supported by one synapomorphy, the shape of the notch for the *peronaeus* nerve in the proximal tarsometatarsus, among 10 defining characters.

Monophyly of the milvines and haliaeetines is supported by 13 characters, including the fusion of the first two phalanges of the second pedal digit. Olson (1982) surveyed the distribution of this derived character in the Accipitridae and reported it in *Ictinia*, *Busarellus*, *Haliastur*, *Milvus*, *Haliaeetus*, and *Ichthyophaga*. These genera occurred in three distinct groups on the trees found here (Fig. 5.1), and the character did not define a small, monophyletic group as proposed by Olson (1982).

It is unclear what functional advantage, if any, is associated with the phalangeal fusion, but at least some members of all three groups take fish, although Olson (1982) rejected any connection with diet or habits. However, he regarded *Ictinia* as a kite, whereas my results indicated that it is related to *Buteo* and *Accipiter* as suggested by Shufeldt (1891) (see below). The absence of fused phalanges in *Pandion*, an obligate fish predator, weakens the argument for their evolution principally for fishing.

As Olson (1982) pointed out, the sequence *Milvus-Haliastur-Haliaeetus-Ichthyophaga* parallels an increasing association with aquatic environments and reliance on a diet of fish. *Buteogallus* is mainly a crab-eater that lives in swampy habitats, and this accords to some extent with its basal position in the clade. The specialised fishing behaviours exhibited by *Busarellus* are, according to my results, convergent on those of the milvine-haliaeetine clade.

5.3.7 *Geranoaetus* and *Heterospizias*

The isolation of *Geranoaetus* (Grey Eagle-buzzard) as a separate clade is supported by 23 characters, including one autapomorphy (Fig. 5.8). Despite the 'identity' of its karyotype with that of *Buteo* (de Boer & Sinoo 1984), *Geranoaetus* appears to be an early offshoot from the buteonine-accipitrine lineage rather than a sub-buteonine as concluded by Amadon (1982b). Its resemblance to the buteonines is probably symplesiomorphic.

Heterospizias (Savannah Hawk) is another isolated South American form (Fig. 5.9) symplesiomorphically similar to the buteonine groups with which it has been linked (Brown & Amadon 1968; Jollie 1977c). It is not close to *Buteogallus*, with which it was synonymised by Amadon (1982b). Following an examination

of osteological characters, Plótnick (1956) concluded that *Heterospizias* was similar to *Buteo* and relatively distant from *Accipiter*, a conclusion which is supported by my results if the resemblance to *Buteo* is considered to be plesiomorphic.

5.3.8 *Aquila*, *Spizaetus*, and *Harpagornis*

Aquila (Golden Eagle group) and *Spizaetus* (South American Hawk Eagles) were independently derived, but adjacent on both trees. Monophyly of the aquiline genera, *Aquila* and *Harpagornis*, was supported by two synapomorphies, one of which was then reversed in *Harpagornis* (Fig. 5.9). The placement of *Harpagornis* as the sister group of *Aquila* was the major finding of this study, with respect to the primary objective of my thesis research. The proximity of the aquilines to the spizaetines makes an examination of the African and south-east Asian taxa presently placed in *Spizaetus* all the more urgent. Brown & Amadon (1968) suggested that the Asian forms may be a separate group, and Jollie (1977c) showed the genus had two parts, which he thought resembled each other "as much through convergence, as through common ancestry" (Jollie 1977c: 117(317).

Harpagornis itself was separated from *Aquila* by two autapomorphies within the Accipitridae as accepted here, although both character states were shared with *Pandion*. One character of the femur was convergent with *Ictinia*, another (of the tibiotarsus) was shared with *Elanus*, and a tibiotarsal character was shared with the *Gyps-Aegypius* clade.

Oliver (1930) concluded that *Harpagornis* was most closely related to *Aquila*, but later (Oliver 1945, 1955) changed his mind and suggested that it was related to *Haliaeetus*: "By the form of the skull, however, it should be placed nearer to *Haliæëtus*. In fact, it is further from *Aquila* than is *Haliæëtus*" (Oliver 1945: 137).

Shufeldt (1896) noted similarities to both *Haliaeetus* and *Aquila*, and placed *Harpagornis* "between" them. My results indicate that resemblances to *Haliaeetus* are symplesiomorphic, and that the bird is an aquiline. However, the closeness of the branch point of the clade to that of the South American

Spizaetus, and the absence of data on Asian *Spizaetus* indicate that further research will be necessary before the group can be understood.

It has been assumed, without substantiation, that *Harpagornis* is most closely to the Australian Wedge-tailed Eagle (*Aquila audax*) (e.g., Duff 1949; Millener 1984). Without a detailed study of the relationships within and between *Aquila* and *Haliaeetus*, however, the sister taxon cannot be identified. Insufficient material of some of the rarer taxa precluded my examining this question.

5.3.9 *Busarellus, Hieraaetus*, and *Polemaetus*

The inclusion of *Busarellus* (Fishing Buzzard) in a clade with a group of African and Eurasian eagles (Fig. 5.10) was unexpected, in view of its present position in the sub-buteonines (Brown & Amadon 1968). The clade is supported by 18 characters, none of which is an unambiguous synapomorphy, however. The clade consisting of *Busarellus* alone is based on 21 characters, of which one is an autapomorphy (Fig. 5.10), and one the apparently convergent fusion of the pedal phalanges discussed above with respect to the milvine-haliaeetine clade. *Hieraaetus* and *Polemaetus* are linked by nine character state changes (Fig. 5.10).

Brown & Amadon (1968) noted that Ridgway (1873) thought that *Busarellus* was isolated, and perhaps close to *Hamirostra* (Australian Black-breasted Buzzard). However, they concluded that "the resemblance to that genus is superficial and the resemblance to the neo-tropical genera just mentioned [*Heterospizias, Buteogallus*, and *Parabuteo*] is real" (Brown & Amadon 1968: 565). Olson (1982) believed that Ridgway's 1873 and 1876 papers were the "last opinion on the matter to be founded on anything other than tradition", and that later works relied on the sequence of genera in Ridgway's publications rather than his stated conclusions. Olson (1982) also pointed out that no characters had been published that justified the linking of *Busarellus* with the sub-buteonines.

The position of *Hieraaetus*, the genus of Eurasian and African Hawk Eagles, has been debated, including whether it should be recognised at all or whether the constituent species should be included in *Aquila* (Brown & Amadon 1968). Its position in my scheme as the sister group of *Polemaetus* is supported by nine characters, including four examples of convergence (Fig. 5.10). Brown

& Amadon (1968) concluded that *Polemaetus* was not close to *Spizaetus* or any other genus, but Amadon (1982a) merged the two under *Hieraaetus*, citing behavioural similarities in evidence. *Polemaetus* was distinguished by a single unambiguous autapomorphy among 20 characters (Fig. 5.10).

5.3.10 The "booted eagles"

Nine genera of large eagles with feathered legs have been recognised as a monophyletic group, but the inclusion of taxa such as *Ictinaetus* has been questioned (Amadon 1982a). Amadon (1982a) submerged one genus in *Hieraaetus* and three in *Spizaetus*.

My results suggest that the "booted eagles" are a paraphyletic grouping of taxa, based on a single character that has been demonstrated to vary even within genera (Amadon 1982a). The submergence of *Stephanoaetus* and *Lophaetus* in *Spizaetus* is not supported by the topology of the tree described here.

5.3.11 Harpies

Recognition of *Stephanoaetus* (African Crowned Eagle) as a sister group of *Harpia* (South American Harpy Eagle) is based on 11 characters, but no unambiguous synapomorphies (Fig. 5.11). *Harpia* exhibited three autapomorphies, but *Stephanoaetus* none.

As noted above, the placement of *Stephanoaetus* in the Harpy clade does not support its submergence in *Spizaetus* (Amadon 1982a; Voous & Wijsman 1964) or even a close relationship with *Spizaetus* as suggested by Brown & Amadon (1968). Brown (1982) resurrected *Stephanoaetus*. However, Amadon (1982a) pointed out some similarities between *Harpia* and *Stephanoaetus* in proportions, habits, a two year breeding cycle, and immature plumage.

Jollie (1977c) grouped *Stephanoaetus* with *Polemaetus* and *Spizaetus*, and apparently separated these and other "aquilins" from the Harpies. However, his diagrams are somewhat ambiguous and the aquilins appear as a sister group of the Harpies in one that details relationships among the accipitrin and buteonine genera.

5.3.12 *Lophaetus, Pithecophaga* and *Morphnus*

Similarities between these geographically widely separated taxa are apparently symplesiomorphic, because all formed separate clades in my tree (Fig. 5.1, 5.11).

My results do not support Amadon's (1982a) lumping of *Lophaetus* and *Spizaetus*. *Lophaetus* (mis-spelled *Lophoaetus* in Amadon & Brown 1968, and in Amadon 1982), the African Long-crested Eagle, was considered to be the sister group of *Spizaetus*, *Polemaetus*, and *Stephanoaetus* by Jollie (1977c).

Pithecophaga forms another monotypic clade. Its karyotype is similar to that of the Aegypiines (de Boer & Sinoo 1984), but its position on my tree suggests that the resemblances may be symplesiomorphic. Shufeldt (1919) concluded that it was related to *Harpia*. Brown & Amadon (1968: 22) also placed it near *Harpia*, although they noted "We do not claim that the New and Old World genera placed in this group [*Pithecophaga, Harpyopsis, Harpia, Morphnus*] have any special or close relationship, but viewed on a worldwide basis they all represent the climax of one line of raptorial evolution". This comment suggests that Brown & Amadon (1968) viewed the Harpies as a grade rather than a phylogenetic group. Jollie (1977c) placed *Pithecophaga* near the gypaetins, but left the proximity of the connection unresolved.

Morphnus (Guianan Crested Eagle) also constitutes a separate lineage on my tree, but it is not particularly close to the Harpies, with which it was grouped by Brown & Amadon (1968) and Jollie (1977c). It differs from *Harpia* in having short, broad wings, and a long tail, which give it the proportions of an *Accipiter*. The karyotype is normal for an accipitrid (Williams & Benirschke 1976).

5.3.13 *Kaupifalco*

Kaupifalco (African Lizard Buzzard) branches off at the base of the accipitrine/buteonine group (Fig. 5.12). Jollie (1977c) placed it beside *Buteo* and *Butastur* (not dealt with here) which, together with *Leucopternis* and *Parabuteo*, formed his paraphyletic 'buteonin core'. Brown & Amadon (1968) thought it near *Buteo*, and that it resembled 'fortuitous[ly]' some species of *Leucopternis*.

5.3.14 *Harpagus* and *Ictinia*

Harpagus (Double-toothed Kite) and *Ictinia* (Mississippi Kites) formed a clade supported by 16 characters, including two unambiguous synapomorphies (Fig. 5.12). Shufeldt (1891) pointed out that the skeleton of *Ictinia* is similar to that of *Buteo*, but Jollie (1977c) included *Ictinia* with the elanin kites, and Brown & Amadon (1968: 20) placed it between the elanin and milvine kites, commenting that it is "like *Milvus* and *Elanus* a classic kite in form". The fused phalanges of the second pedal digit are apparently convergent with those of *Busarellus* and the milvines and haliaeetines (see above).

L Miller (1937) pointed out that *Harpagus bidentatus* has been placed in both the Falconidae (by Carriker and Bowdler Sharpe) and the Accipitridae (by Peters). Suschkin (1905) rejected a relationship with the Falconidae, a contention based mainly on the denticulate bill, and Miller (1937) pointed out several osteological features that support its being an accipitrid resembling *Accipiter* more than *Elanus*. He placed it "between" *Elanus leucurus* and *Accipiter cooperii*.

Amadon (1961), however, argued that *Harpagus* is a kite, and he rejected similarities to *Accipiter* as coincidental or the result of mimicry. Later he suggested that, despite reports that the bird hunts like an *Accipiter*, it is probably 'kite-like' in the way it hunts lizards and large insects (Amadon 1964). However, he also pointed out that it resembles *Accipiter* in being strongly sexually dimorphic in size.

Harpagus was separated from *Ictinia* by two autapomorphies among 31 character state changes.

5.3.15 *Melierax*, accipiters, and the buteos

Melierax (African Chanting Goshawks) and the accipiters and buteos are supported as a monophyletic clade by 10 characters, including one unambiguous synapomorphy (Fig. 5.12, 5.13). Brown & Amadon (1968) placed *Melierax* between *Circus* and the accipiters, but noted that its relationships are not obvious.

Buteo (Buzzards) and *Accipiter* (Sparrowhawks and Goshawks) are the most speciose genera in the family (Stresemann & Amadon 1979). Their close

relationship was pointed out by Brown & Amadon (1968). Jollie (1977c) also placed them near each other, and included *Leucopternis* (American White Hawks) and *Erythrotriorchis* (Australian Red 'Goshawk') in the group. Both he and Brown & Amadon (1968), however, linked *Erythrotriorchis* with *Accipiter* rather than with *Buteo* as in the present tree (Fig. 5.13).

On my tree *Leucopternis* is the sister group of a clade composed of *Buteo*, *Parabuteo* (American Bay-winged Hawk), and *Erythrotriorchis*, and so branches off between *Accipiter* and *Buteo*. Brown & Amadon (1968) concluded that *Leucopternis* is related to *Buteo*. Jollie (1977c) made it a sister group of *Parabuteo*, judging from his diagram, and together with *Geranospiza*, he linked them with *Buteo* on one side and *Accipiter* on the other.

Parabuteo is the sister group of the *Buteo-Erythrotriorchis* clade (Fig. 5.13). Brown & Amadon (1968) concluded that it was very close to *Buteo*. However, they also raised the possibility of a relationship with *Heterospizias* and *Buteogallus*. Later, Amadon (1982b) chose to ally *Parabuteo* with *Heterospizias*, and he synonymised in turn *Heterospizias* with *Buteogallus*. These genera are widely separated in the tree found here, and their synonymy is not supported.

My phylogenetic tree indicated that *Erythrotriorchis* is related to *Buteo* and not to *Accipiter* (Fig. 5.13). In contrast, Amadon (1978) synonymised *Erythrotriorchis* with *Accipiter*, even though he pointed out it that resembles *Buteo* in proportions, especially in having longer wings.

Olson (1987) discussed the distribution of the procoracoid foramen in the Accipitridae. He found it to be invariably absent in *Accipiter*, nearly or completely absent in some individuals of *Harpagus* and *Circus*, but present in others. Examination of a specimen in the British Museum (Natural History) (Blandamer & Burton 1979) revealed a fully developed procoracoid foramen. The amount of variation in the condition of the procoracoid foramen in *Erythrotriorchis* will be impossible to ascertain until further specimens are obtained, but the evidence presented here indicates that *Erythrotriorchis* is not a synonym of *Accipiter*. Furthermore, the proximity of *Accipiter* to *Buteo* demonstrated by my tree makes the argument as to whether *Erythrotriorchis* is closer to one or the other somewhat trivial.

5.3.16 DNA-DNA hybridisation

Sibley & Ahlquist (1990) presented a phylogenetic tree for the class Aves, based on DNA-DNA hybridization data. The tree included one species of each of seven genera of Accipitridae (*Gyps, Aegypius, Neophron, Gypaetus, Harpagus, Accipiter*), two species of an eighth (*Buteo*), four of a ninth (*Circus*), *Pandion* and *Sagittarius*. The topology of their tree is very similar to mine, except for the position of *Circus* (put as the sister group of *Harpagus* as against a near-basal clade in mine), and details of the branching within the vultures.

Sagittarius is basal in the Sibley & Ahlquist tree, separated from *Pandion* by 2.6 $_{\Delta}T_{50}$ units[1]. *Pandion* itself is separated from the accipitrids by 2.6 units. The vultures are then 1.2 units, and the other accipitrids 0.6 units, from the common node with *Pandion*.

In the vultures, the distance between *Gyps* and *Aegypius* is not resolved, and *Neophron* and *Gypaetus* are sister groups. In the other major clade, *Accipiter* is the sister group of the two *Buteo* species as in my tree, and *Harpagus* is a sister group of *Circus*. Given the few taxa involved, the correspondence between the two trees is remarkably good.

5.3.17 Mallophaga

Clay (1951) used the distribution of taxa of Mallophaga (bird lice) to argue that the Falconiformes is a monophyletic group. Other evidence (see Introduction to this chapter; 5.1) suggests that this is not correct. The distribution of genera such as *Laemobothrium*, which occurs on both accipitrid and vulturid vultures (Nelson & Price 1965) probably results from the long sympatry of the two vulture groups in North America and Europe (Cracraft & Rich 1972; Rich 1980).

Within the Accipitridae as understood here, however, the distribution of species in the genus *Degeeriella* has been used to elucidate intrafamilial relationships (Clay 1958). Although most genera of Accipitridae appear to have their own species or subspecies of *Degeeriella*, the presence of particular species

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[1] $_{\Delta}T_{50}$ is the difference between the temperature at which all DNA is single chain, and the temperature at which 50% of the DNA has formed duplexes.

groups of Mallophaga may indeed reflect major groupings in the Accipitridae (Fig. 5.14A). This may be so even though there are difficulties in relating character differences in the lice to separation times of the host taxa (Clay 1958).

The elanid and elanoidid kites share species of the *D. elani* species group (Clay 1958). Members of this group are also found on *Chelictinia* (African Swallow-tailed Kite) and *Aviceda* (Crested Hawks), which are not included in my phylogenetic tree because of insufficient data, although the *Degeeriella* on *Aviceda* is less certainly related to others of the *elani* group (Clay 1958). A species of the *elani* group also occurs on *Gampsonyx* (American Pearl Kite), which Clay incorrectly included in the Falconidae; *Gampsonyx* was later shown to be an accipitrid (Brodkorb 1960).

Pernis, traditionally placed with the kites, hosts lice of a different species group (*phlyctopygus*) and members of the *elani* species group are absent (Clay 1958). The *phlyctopygus* group apparently shows affinities to the *regalis* species group taxa characteristic of the milvine kites, and *Haliaeetus* (Clay 1958). *Ichthyophaga* and *Buteogallus* have species of the *fulva* group instead, possibly a plesiomorphic condition, as the *fulva* group is the only one known on most genera of the sister clade to the milvines (Fig. 5.14A). The only exceptions are the presence of lice of the *discocephalus* species group on *Aquila* and one species of *Haliaeetus*, and the *regalis* group on two species of *Buteo* (Clay 1958) (Fig. 5.14A). The presence of *discocephalus* lice on two northern species of *Haliaeetus* may be the result of contact between *Aquila* and *Haliaeetus* at feeding sites in winter when food supplies are restricted.

Members of the *fulva* group are also found on species of the Serpent Eagle clade (Fig. 5.14B). The presence of the distinctive *punctifer* group on both *Gyps* and *Gypaetus* (Clay 1958) is a derived character supporting their relationship as depicted in Fig. 5.4-5.5. However, the presence of a *regalis* louse on *Gypohierax* (Fig. 5.14C) is apparently either a plesiomorphic feature, or the result of host transfer.

In general, the distribution of the species groups of *Degeeriella* provides independent support for the topology of my phylogenetic trees based on osteological data. Species of the *elani* group seem to be associated with taxa

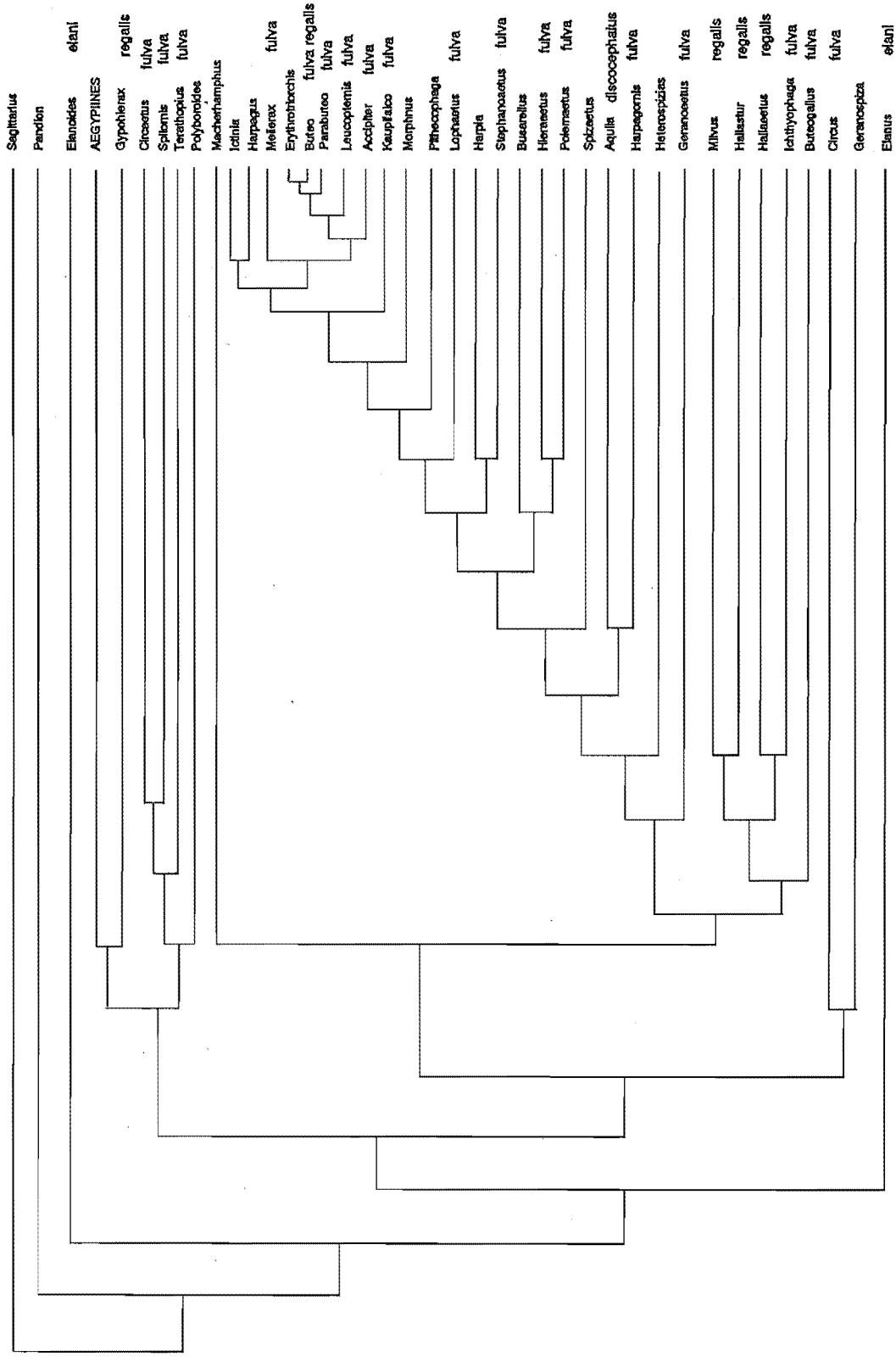

Fig. 5.14A Phylogenetic tree of the Accipitridae, showing the species groups(e.g., *elani*) of *Degeeriella* (Insecta: Mallophaga) to which each genus is host (from Clay 1958).

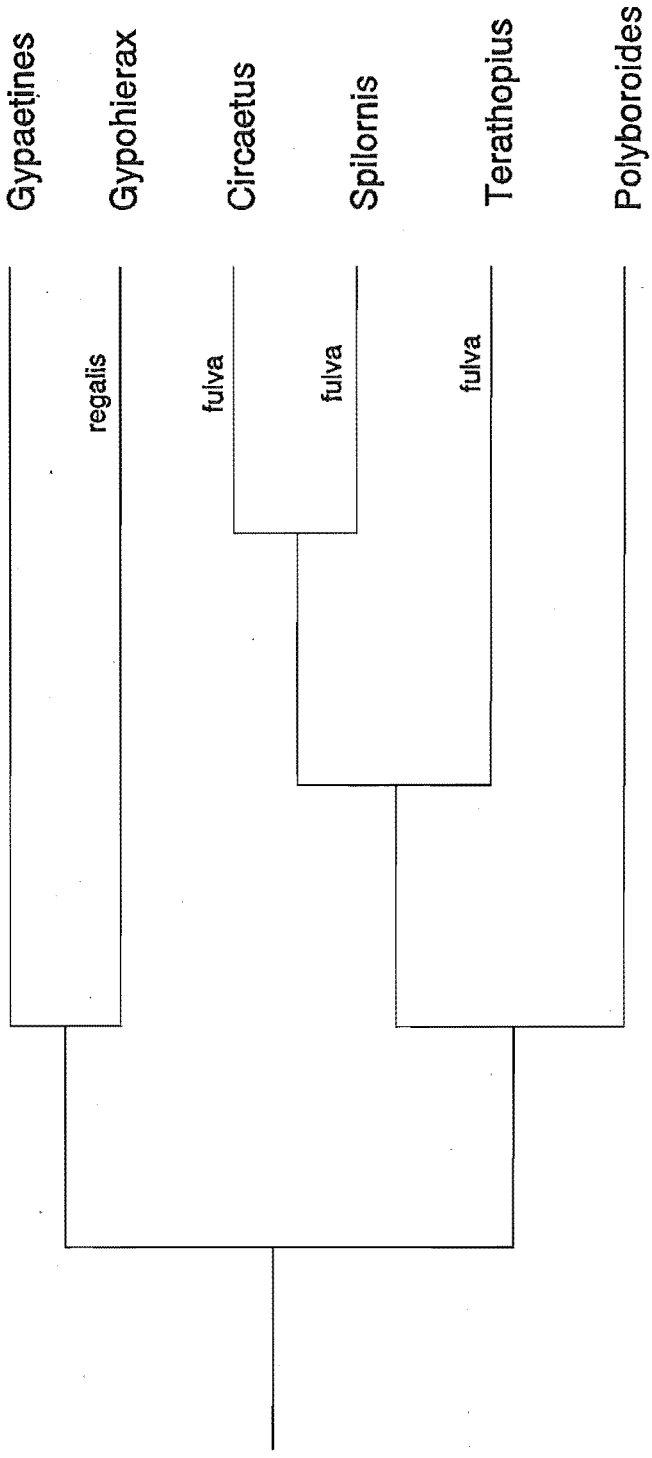

Fig. 5.14B Phylogenetic tree of the gypaetines and snake eagles, showing the species groups of *Degeeriella* (Insecta: Mallophaga) to which each genus is host (from Clay 1958).

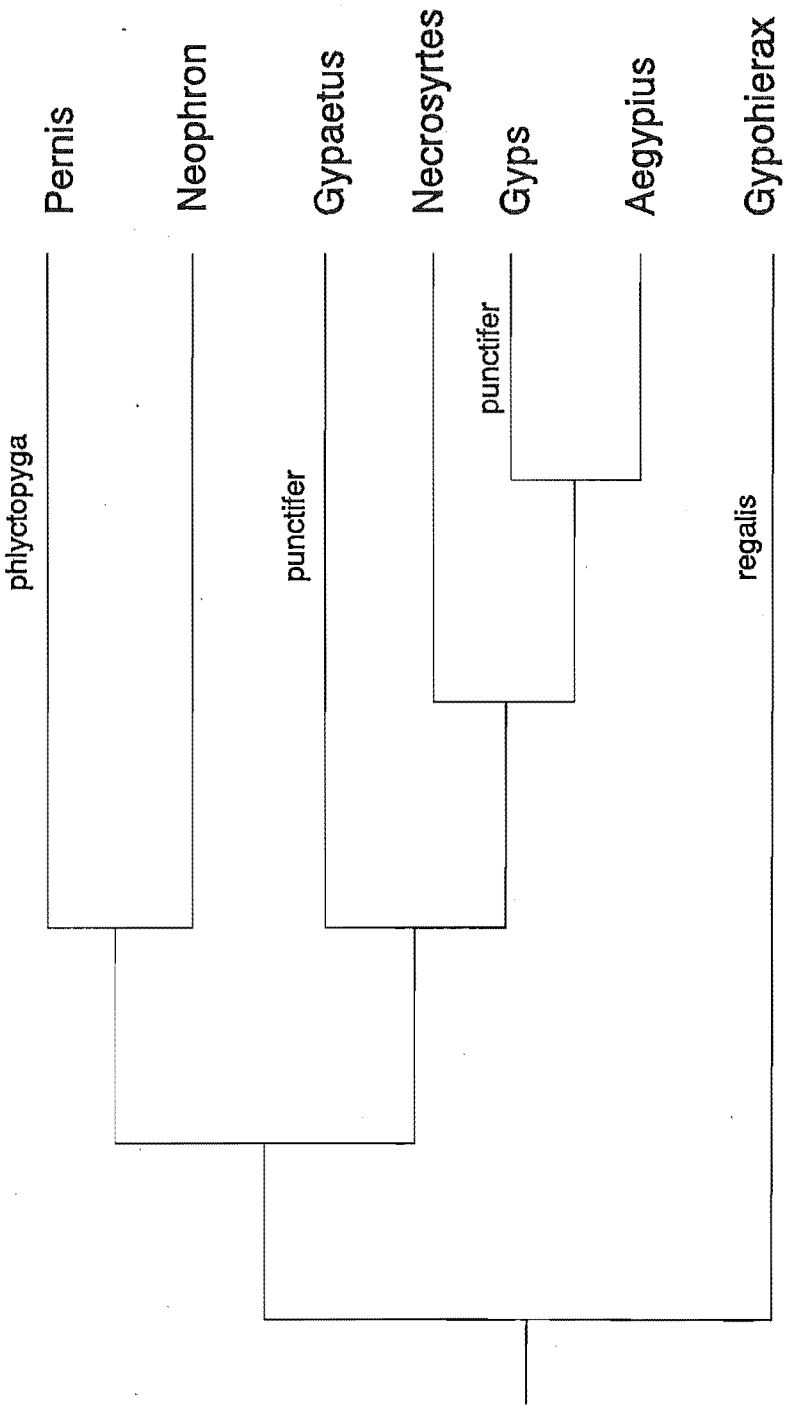

Fig. 5.14C Phylogenetic tree of the gypaetines/aegypiines, showing the species groups of *Degeeriella* (Insecta: Mallophaga) to which each genus is host (from Clay 1958).

isolated by the initial radiation of accipitrids and represented today by the elanin and elanoidin kites and the Crested Hawks.

Possession of the *fulva* group is a plesiomorphic feature of accipitrid genera, and the presence of *regalis*, *discocephalus*, and *punctifer* groups are derived features of the milvins, aquilins, and gypaetins, respectively. The *phlyctopyga* group appears to be autapomorphic for *Pernis*. Its presence on *Neophron* would provide strong supporting evidence for the branching pattern of the tree presented here.

5.3.18 Biogeography

The Accipitridae is a cosmopolitan family, absent only from Antarctica and some remote oceanic islands (Brown & Amadon 1968). An inspection of the species distributions given by Stresemann & Amadon (1979) shows, however, that there is considerable heterogeneity in the representation of different genera in different regions. A tree of the relationships among operational geographic units (OGUs) derived from the taxon distribution matrix (Appendix 5.4) using PAUP and South America as the designated ancestor, is shown in Fig. 5.15. The geographic areas used are shown in Fig. 5.16.

The tree can be viewed as linking centres of diversity in South America and Africa, with intermediate areas exhibiting mixes of taxa in proportion both to their distance from each centre, and to the relative vagility of the taxa. The second factor is exemplified by the accipitrid faunas of New Zealand, Greenland, and Oceania. The major, or only, groups in these areas are the *Haliaeetus* eagles, *Circus*, and the occasional *Aquila*-type (New Zealand), *Buteo* (Galapagos and Hawaii), and *Accipiter* (Fiji, but this is linked by islands to Melanesia and there are no major water crossings involved in reaching the archipelago). These are the only genera whose species seem to be able, or willing, to cross large water gaps, and they are the most cosmopolitan of the accipitrids.

South-east Asia and the Indo-Philippine islands are 'sister groups', whose accipitrid faunas are linked to Australia and to Asia north of the Himalayas and from there to Europe, and Africa; but they have little in common with the North American fauna (Fig. 5.15). The distribution of apparently relict taxa across the

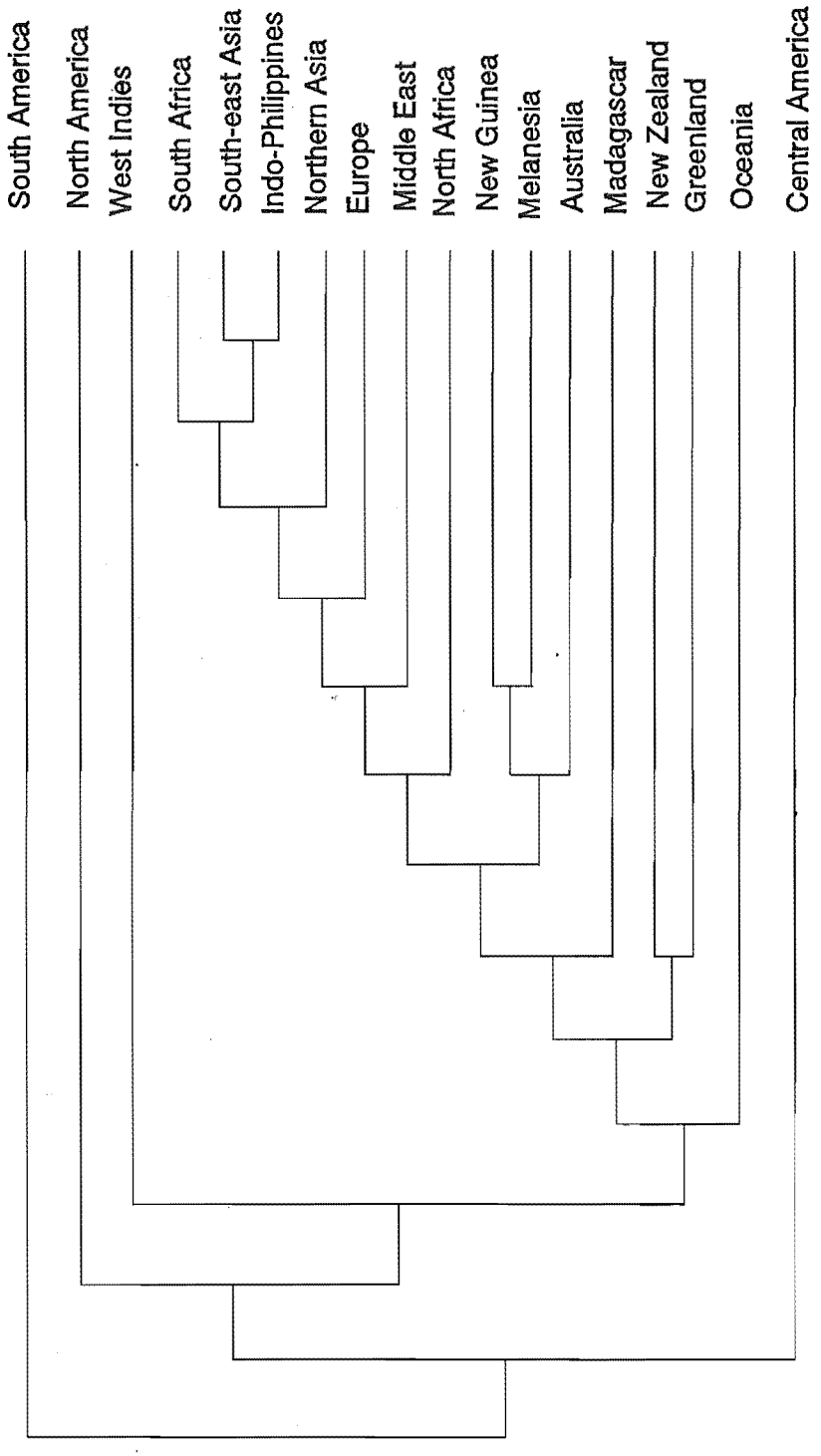

Fig. 5.15 Biogeographic tree of the Accipitridae, using areas as taxa, genera as characters (with numbers of species as character states). See Appendix 5.4 for taxa and areas and Fig. 5.16 for regions used.

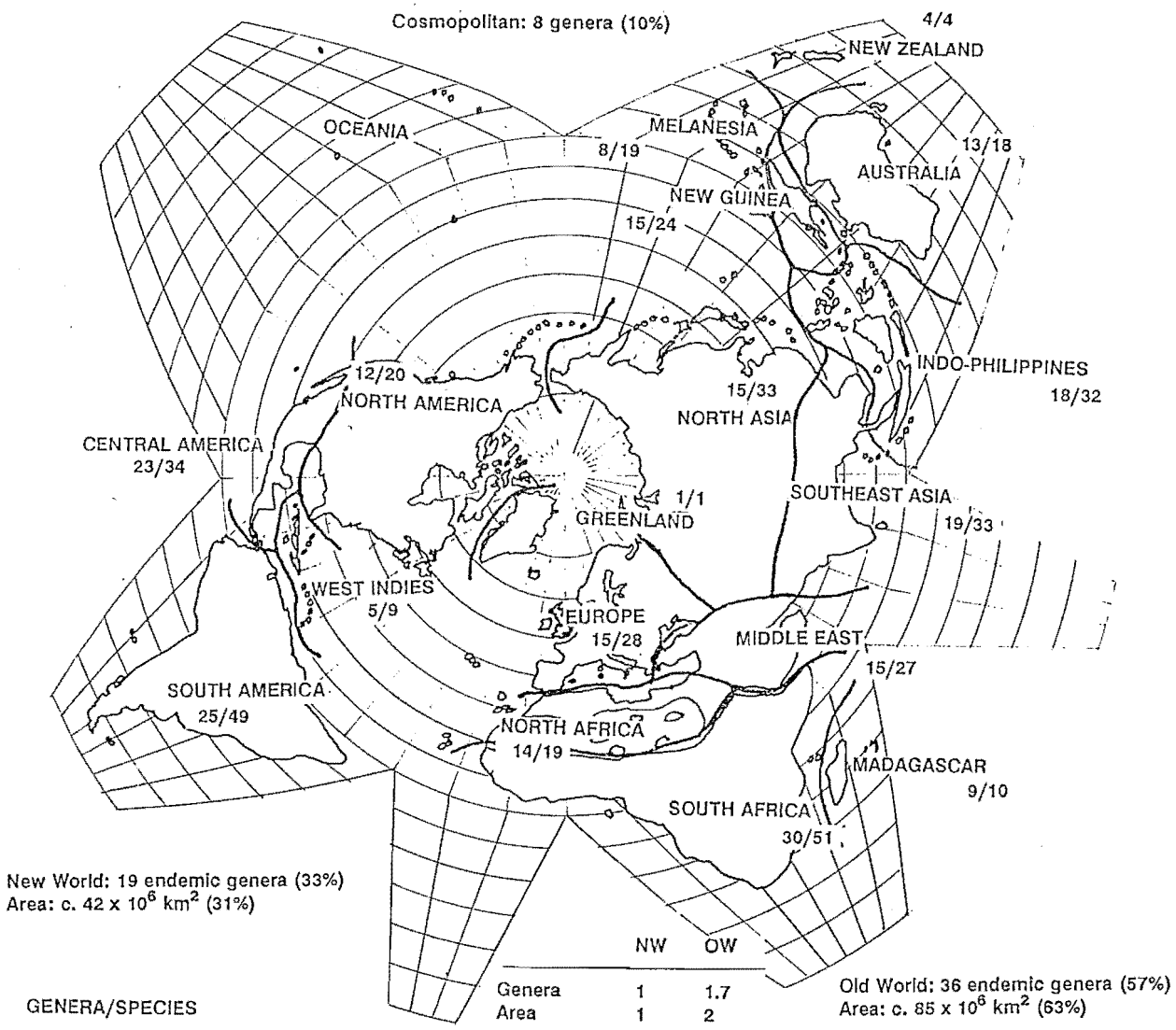

Fig. 5.16 Map of biogeographic regions used in this study. See Appendix 5.4 for number of species and genera in each region.

now widely separated land masses of the southern hemisphere, and the inability of most accipitrids to cross large water gaps suggest that these taxa have been isolated by movement of land masses during the birds' evolutionary history. A corollary is that the taxa are old. The oldest accipitrids known are late Eocene to early Oligocene in age, but buteonine hawks do not appear in the fossil record until the middle Miocene of Europe (Olson 1985).

If the accipitrids radiated during the Oligocene, then the position and movement of continental blocks from the Oligocene to the present may have influenced or helped drive the evolution of the group. Sea gaps between Australia and Antarctica and Antarctica and South America were very much narrower during the Oligocene than they are today, according to Owen's (1983, map 66) map of continental positions 29 million years BP.[2] Antarctica and the Falkland Islands had extensive forests at that time (Birnie & Roberts 1986; Rich 1975), and the environment would have favoured the spread of birds from South America to Australia or vice versa. Antarctica itself may have been the site of much bird evolution, of which there is presently no known fossil record (Rich 1975).

Africa had separated from both South America and Antarctica millions of years before they separated from each other (Owen 1983), and the faunal links between Africa and the others are much more distant. It was effectively isolated from both South America and Antarctica-Australia by wide oceans or long distances by land during the Oligocene.

The long-held view that birds colonised Australia from the north (e.g., Mayr 1944) has been refuted by systematic work showing that an independent radiation of the passerines produced groups convergent on Palaearctic families (Sibley & Ahlquist 1985). Much of the evolutionary history of the Accipitridae may have occurred on southern land masses, including Antarctica. The presence of endemic taxa such as *Lophoictinia*, *Hamirostra*, and *Erythrotriorchis* suggests that not all accipitrids have colonised Australia from elsewhere.

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[2]Owen's reconstructions were rejected by Cox (1990), but Owen (1990) argued strongly that the objections were based on poor cartographic techniques.

The Australian fossil record includes several accipitrids of up to mid-Miocene age (Rich & Baird 1986), but these, including a supposed gypaetin vulture, are of uncertain relationships (Rich & van Tets 1982).

Large accipitrids are known from the Australian Quaternary (Rich & van Tets 1982; Rich & Baird 1986), but the association Rich & Baird (1986) make between large size and scavenging habits is unproven.

Australia had extensive rain forests until the late Quaternary (Rich 1975), and the barriers to forest birds formed by the hot desert of Australia and the cold desert of Antarctica are relatively new. Present forest areas in New Guinea, Southeast Asia, and South America were linked by others in the geologically recent past. Links between isolated forest taxa such as *Harpyopsis* of New Guinea and *Pithecophaga* of the Philippines may be better sought to the south rather than the north. Indeed, Rich & van Tets (1982) reported that a small fossil eagle (*Necrastur alacer*) from the Australian Pleistocene resembled *Harpyopsis*.

The poor pre-Quaternary fossil record of accipitrids in Australia (Rich & Baird 1986), and present total absence of such a record in New Zealand (Fordyce 1982) makes a definitive statement on the origin of Haast's Eagle impossible. Its sister group relationship with *Aquila* suggests that it may be a relatively recent immigrant from Australia, but little is known about the time of radiation or dispersal of the *Aquila* eagles, or even how long *Aquila audax* has been in Australia. Rich & van Tets (1982) suggested that one of the large Quaternary accipitrids was similar in size to Haast's Eagle, and that another species, smaller than "*Harpagornis assimilis*", had bones of similar shape to those of Haast's Eagle. This material warrants further study.

The ancestor of Haast's Eagle may have arrived as early as the Early Miocene, when the New Zealand forests were similar to those in highland New Guinea today (Pocknall 1989).

5.4 DISCUSSION

5.4.1 Relationships of Haast's Eagle

The principal result of my analysis is the placement of Haast's Eagle as sister group of *Aquila*, the genus containing the Golden and Wedge-tailed Eagles

(*Aquila chrysaetos* and *A. audax*) (Stresemann & Amadon 1979). A relationship with *Aquila* conflicts with Oliver's (1945, 1955) conclusions, but is in accordance with one popularly held view of Haast's Eagle's relationships (e.g., Duff 1949). Brathwaite's hypothesis that Haast's Eagle belonged with *Spizaetus* could not be refuted or supported because of the paucity of material of South-east Asian *Spizaetus*. However, a South American *Spizaetus* is next to *Harpagornis* on my phylogenetic tree.

5.4.2 The phylogenetic tree

I did not expect to derive a single principal tree topology from the array of qualitative osteological characters used. Livezey (1986) found 50 equal-length trees for the Anseriformes, using 120 characters that for the most part were established, and ordered transition series. However, Siegel-Causey (1988) obtained one tree from 137 characters for 30 species.

The overall consistency indices for both these studies were much higher than found here. There could be the result of my characters being less well defined, the complexity of the variation within the group (Jollie 1976, 1977a, 1977b, 1977c), and the short time available to me with collections, and of the large number of taxa. It was less easy to 'mine' the literature for characters, because previous studies (e.g., Amadon 1953, 1978, 1982a, 1982b; Brown 1982; Brown & Amadon 1968; Friedmann 1950) concentrated on details of bill, legs, and wing and tail proportions.

Archie (1989) questioned the value of consistency indices (Kluge & Farris 1969) as measures of the efficiency of the analysis, who emphasised the inverse relationship between the number of taxa studied and the consistency index, and between the consistency index and the number of characters.

The consistency index obtained here (0.217), although low, is consistent with those of analyses of more than 40 taxa, using well over 100 characters (Archie 1989, fig. 5a). The number of steps per character (8.9) was above those given for missing value data, but less than for 2-state data. However, if Archie's (1989) fig. 1 plots are extrapolated to 45 taxa (as used here), there is closer agreement in number of steps per character.

While the low consistency index may result largely from intrinsic properties of large data sets, examination of the character state changes suggests that evolution within the group has been by changes in suites of minor features within historical, phylogenetic, and broad functional constraints (Seilacher 1979).

Homoplasies and character-state reversals rather than absolute synapomorphies characterise most clades within the Accipitridae. Superficial resemblances in external characters have often formed the basis of classifications within and between genera (Amadon 1982b - sub-buteonines; Wattel 1973 - accipiters), but these were shown to reflect adaptation to a limited range of niches available for raptors. An indication of the ability of different lineages to give rise to ecological correlates is the strong external resemblance of *Ictinia* to the *Elanus* kites in colour pattern, proportions, and behaviour. In its skeleton, as Shufeldt (1891) noted long ago and was confirmed here, *Ictinia* is very close to *Buteo*.

External resemblances of phylogenetically distinct lines have resulted in the complex and fluid higher taxonomy of the Accipitridae (reviewed by Sibley & Ahlquist (1972)). A feature of the tree presented here is the association of groups of species long thought to be related on general resemblances, such as the milvine kites and sea eagles and the accipitrid vultures and serpent eagles.

Although it is comforting that the tree topology incorporates existing arrangements, this is not a valid test of the hypothesised relationships presented here. Indeed, Panchen (1982) has argued that parsimony, the basic assumption of the techniques used here, is inconsistent with the hypothetico-deductive model of science, as championed by Popper (1959) and there is no satisfactory test of such trees.

I believe, however, that my results suggest that a cladistic approach may be useful resolving some of the more controversial aspects of accipitrid relationships, despite Jollie's (1976) doubts. At the very least, the topology of my accipitrid phylogenetic tree may be a source of hypotheses that can guide future work. With our present profound ignorance of the relationships within and without the family (Olson 1985), no approach should be dismissed completely.

5.4.3 Choice of characters

The features chosen for this study tended to be those that described the shape and structure of individual elements, so that they could be of maximum use for analysis of fossil taxa. Some were more'descriptive' than is usual in comparative morphology. All features used displayed recognisable variation within the group, or between the group and the outgroups used and therefore can be considered as characters suitable for analysis by maximum parsimony techniques.

That the analysis converged on two closely similar trees (differing only on the position of a single taxon within a major clade) without a priori or a posteriori weighting of features suggests that noise from 'poorer' characters was overcome by the use of large numbers of features. For an exploratory study such as this, use of many characters can not only result in the discovery of basic pattern as a guide to forming hypotheses on smaller subsets more amenable to analysis, but also allows an evaluation of the variability of new characters.

5.4.4 Raptor ecology and homoplasy

A major feature of the analysis was the complex nature of the variation in character states. This was apparent in recognised features such as the procoracoid foramen as well as in less well defined characters identified in my examination of the material. The frequent reversals reflect the limited variance in structure within the group, and the way morphologies have been mixed and matched in different lineages. Symplesiomorphies were found to be a major source of confusion in discerning intrafamilial relationships.

5.4.5 Level of treatment

My use of the genus as the basic OTU assumed that generic level systematics of the Accipitridae were well founded. This is probably not a valid assumption because the limits of several genera are blurred by frequent changes in taxonomy, particularly in *Spizaetus* and African forest eagles (e.g., Amadon 1982a). However, my sample represented most of the major variation amongst c 220 species in the family (Stresemann & Amadon 1979).

5.4.6 Methodological limitations

Most of the problems with assessing character states for taxa resulted from the state and availability of specimens. Apart from the taxa that were not available in any institution, others were represented by incomplete specimens or sometimes a few bones. Others were incompletely prepared, and characters were obscured. Many taxa, especially of large eagles and vultures were represented by captive specimens that had evidence of damage or disease associated with captivity. Some had osteoarthritic lesions that obscured characters of the lower leg bones, and several had healed broken wings.

5.4.7 Taxonomic conclusions

Although the main object of this part of my study was to identify the sister group of Haast's Eagle, some more general conclusions on the classification within the Accipitridae may be drawn.

Sagittarius and *Pandion* were found to be sufficiently distinct in their osteology to warrant maintaining them as at least families. My study did not include other non-accipitrids so it the proximity of *Sagittarius* to the accipitrids could not be assessed. From the profound differences in osteology, it is likely to be a distant relationship.

As has been suspected, the 'kites' proved to polyphyletic within the family, representing a grade rather than a clade. *Elanus*, *Elanoides*, and *Ictinia* demonstrate how closely convergent external morphologies can be in different clades, through homoplasy and plesiomorphic traits associated with an insectivorous and lower vertebrate diet.

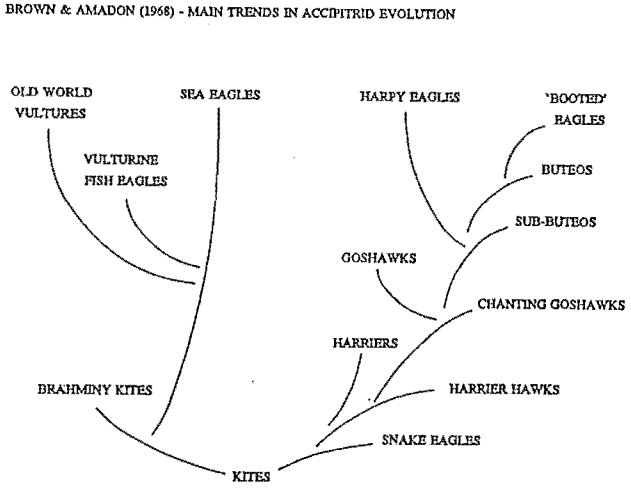
My phylogenetic tree provides at least partial support for Brown & Amadon's (1968) suggestion that omnivorous and scavenging kites and *Pernis*-like species are the least advanced members of the family. Brown & Amadon's 1968) hypothesis that the adaptive radiation of the Accipitridae reached various 'culmination points' in, for example, the accipitrid vultures, the harriers (*Circus*) of open country, bird-catching *Accipiter*s, and swift eagles (such as *Spizaetus*), and other large eagles (such as *Harpia*) is supported in that each of these groups represents a clade on my phylogenetic tree. However, the relationships within the

FRIEDMANN (1950) **A**

ORDER FALCONIFORMES	
SUBORDER FALCONES	
Family SAGITTARIIDAE	Secretary bird
Family PANDIONIDAE	Osprey
Family ACCIPITRIDAE	
Subfamily ELANINAE	Kites
Subfamily PERNINAE	Honey buzzards
Subfamily MILVINAE	Pariah kites
Subfamily ACCIPITRINAE	Hawks
Subfamily BUTEONINAE	Buzzards
Subfamily CIRCINAE	Harriers
Family FALCONIDAE	Falcons
SUBORDER CATHARTAE	
Family CATHARTIDAE	'New World' vultures

BROWN & AMADON (1968) **B**

ORDER FALCONIFORMES
- SUBORDER CATHARTAE
  - Superfamily CATHARTOIDEA
    - Family CATHARTIDAE
- SUBORDER ACCIPITRES
  - Superfamily ACCIPITROIDEA
    - Family PANDIONIDAE
    - Family ACCIPITRIDAE
  - Superfamily SAGITTAROIDEA
    - Family SAGITTARIIDAE
- SUBORDER FALCONES
  - Family FALCONIDAE



STRESEMANN & AMADON (1979) **C**

ORDER FALCONIFORMES
- SUBORDER CATHARTAE
  - Family CATHARTIDAE
- SUBORDER ACCIPITRES
  - Family ACCIPITRIDAE
    - Subfamily PANDIONIDAE
    - Subfamily ACCIPITRINAE
- SUBORDER SAGITTARII
  - Family SAGITTARIIDAE
- SUBORDER FALCONES
  - Family FALCONIDAE
    - Subfamily POLYBORINAE
    - Subfamily FALCONINAE

Fig. 5.17 (A-C) Some recent classifications of the diurnal birds of prey: **A**, Friedmann (1950); **B**, Brown & Amadon (1968), with a chart of suggested main trends in evolution; **C**, Stresemann & Amadon (1979).

Buteo-Accipiter clade are more complex, so all the eagles, *Buteo*s and *Accipiter* cannot be separated in this way.

To summarise the information in my preferred phylogenetic tree, I include a tentative classification of the Accipitridae. The conventions of Wiley (1981) were followed, so that the order of the branching is reflected by the list, with the earlier major clades recognised by Linnaean-style inclusive group names to tribal level. This classification goes to a much lower taxonomic level (tribe) than other recent treatments (Fig. 5.17) to emphasise what I see as potentially the most fruitful areas for future research.

5.5 CLASSIFICATION OF THE ACCIPITRIDAE - BASED ON THE PHYLOGENETIC TREE PRESENTED HERE (using conventions suggested by Wiley (1981)

Order Ciconiiformes (*sensu* Sibley & Ahlquist 1988)

Family Pandionidae (Sclater & Salvin, 1873)
Family Accipitridae (Vieillot, 1816)
Subfamily Elanoidinae Shufeldt, 1891
Elanoides
Subfamily Elaninae Blyth, 1849
Elanus
Gampsonyx (incertae sedis)
Chelictinia (incertae sedis)
Subfamily Gypaetinae Vieillot, 1816
Tribe Gypaetini Vieillot, 1816
Gypohierax
Pernis
Neophron
Gypaetus
Necrosyrtes
Aegypius
Gyps
Tribe Circaetini Blyth, 1849
Polyboroides
Terathopius
Spilornis
Circaetus
Subfamily Circinae Bonaparte, 1838
Circus
Geranospiza
Subfamily Machaerhamphinae **new name**
Machaerhamphus

Subfamily Milvinae Vigors, 1824
Tribe Buteogallini **new name**
Buteogallus
Tribe Milvinae Vigors, 1824
Milvus
Haliastur
Haliaeetus
Ichthyophaga
Subfamily Accipitrinae (Vieillot, 1816)
Geranoaetus
Heterospizias
Aquila
Harpagornis†
Spizaetus
Busarellus
Hieraaetus
Polemaetus
Harpia
Stephanoaetus
Lophaetus
Pithecophaga
Morphnus
Kaupifalco
Ictinia
Harpagus
Melierax
Accipiter
Leucopternis
Parabuteo
Buteo
Erythrotriorchis

The higher classification of Haast's Eagle therefore becomes:

Order Ciconiiformes
Family Accipitridae
Subfamily Accipitrinae
Genus *Harpagornis* Haast, 1872
Harpagornis moorei Haast, 1872

If the higher classification of Sibley & Ahlquist (1988) is not followed, the ordinal name should be Accipitriformes (Vieillot), as listed by Brodkorb (1964).

Appendix 5.1 Features evaluated for and used (bold type) in preliminary and final runs of PAUP (Swofford 1984). (Features used in PAUP analysis coded in bold type.)

No.	Code	Feature [codes for feature states and intermediates]
1	CR1	Median ridge of palatal surface of rostrum: a, obliterating median groove; b, not obliterating groove [a/0 b/1]
2	**CR2**	Palatal processes of premaxilla: a, fused together; b, free; c, bony septal bar; d, in contact, not fused; e, in contact anteriorly, fused posteriorly [a/0 a-b/1 b/2 c/3 d/4 e/5]
3	CR3	Tip of vomer: a, not bridging gap between palatine processes of premaxilla; b, bridging gap [a/0 b/1]
4	**CR4**	Maxillo-palatines and palatines: a, not widely separated or with strong rostral bar; b, widely separated, with strong rostral bar [a/0 b/1]
5	CR5	Posterolateral angle of palatine: a, square, long parallel margin; b, tapered to pterygoid process; c, evenly rounded; d, rounded and notched [a/0 b/1 c/2 d/3]
6	CR6	Palatine fossa: a, not excavated, no choanal ridge; b, well excavated, strong choanal ridge medially [a/0 b/0]
7	CR7	Vomer: a, absent; b, thin, laterally compressed splint; c, slender, with anterior knob; d, nearly tubular, inflated [a/0 b/1 c/2 d/3]
8	CR8	Posteropterygoids: a, clasping parasphenoid rostrum; b, not clasping rostrum [a/0 b/0]
9	CR9	Dorsal surface of maxillopalatine processes: a, fused with ventral wall of vestibule; b, free, forming lateral part of vestibule floor [a/0 b/1]
10	**CR10**	Prefrontal: a, free; b, in contact with frontal and with lateral ethmoid but not fused; c, fused with frontal and with lateral ethmoid [a/0 b/1 c/2]
11	**CR11**	Orbital process of prefrontal: a, curved posteriad; b, flat, spatulate; c, curved rostrad; d, straight [a/0 b/1 c/2 d/3]
12	**CR12**	Posterior margin of supraorbital process of prefrontal: a, pointed to attenuated; b, squared off or notched; c, inflated [a/0 b/1 c/2]
13	CR13	Superciliary: a, present, well-developed; b, absent or rudimentary [a/0 b/1]
14	**CR14**	Lateral wall of nasal vestibule: a, not, or poorly, ossified; b, ossified [a/0 b/1]
15	**CR15**	Zygomatic process of squamosal: a, well-developed; b, absent or rudimentary; c, present but reduced [a/0 b/1 c/2]
16	**CR16**	Articular process of squamosal: a, well-developed; b, absent or rudimentary [a/0 b/1]
17	**CR17**	Tympanic margin: a, not flared; b, flared laterally into a more or less rectangular plate; c, flared into curved plate; d, straight, rostrad [a/0 b/1 c/2 d/3]
18	**CR18**	Basipterygoid processes: a, usually present in adults; b, absent; c, rudimentary [a/0 a-b/1 b/2 c/3]

19 CR19 Posterior tympanic process: a, present, simple; b, absent; c, forming 'cup' around quadrate articulation [a/0 b/1 c/2]

20 CR20 Median basiparasphenoid process: a, absent; b, median tubercle at caudal end of a median ridge; c, several, separated, tubercles; d, irregular transverse ridge [a/0 b/1 c/2 d/3]

21 CR20A Lateral basiparasphenoid process: a, absent; b, a ridge; c, a prominent swelling [a/0 b/1 c/2]

22 **CR21** Interorbital septum: a, perforate; b, small perforation; c, imperforate [a/0 b/1 c/2]

23 CR22 Constriction of nasal vestibule towards middle naris: a, nil; b, slight; c, distinct [a/0 b/1 c/2]

24 CR23 Quadrate articular surface: a, 'normal'; b, smoothly rounded, blending with ventral surface; medial articular surface narrow, extending along caudal margin nearly to caudal angle [a/0 b/1]

25 CR24 Small notch in quadrate: a, absent; b, present [a/0 b/1]

25A **CR25** Postorbital process: a, broad, flat in lateral view; b, pointed, attenuated to a spike [a/0 b/1]

26 **MA1** Median articular processes: a, concave ventrally; b, convex ventrally [a/0 b/1]

27 **MA2** Mandibular rami: a, bent ventrad then rostrad near distal end; b, curving ventrad, then rostrad in symphysis; c, curved evenly ventrad from at least half-way to tip [a/0 b/1 b-c/2 c/3]

28 **MA3** Median articular process: a, with ventrocaudal flange; b, no flange [a/0 b/1]

29 **MA4** Small tubercle (continuation of linear muscle scar running dorsoventrad across internal angle of ramus at articulation): a, present; b, absent; c, ridge [a/0 b/1 c/2]

30 **MA5** Tubercle on median proximal face of ramus, at dorsal edge of angular: a, absent; b, small; c, large [a/0 b/1 b-c/2 c/3]

31 **MA6** Tubercle in MA5: a, so far caudal as to be on dorsal edge, giving extra tubercle there; b, in line with coronoid process; c, between coronoid and surarticular processes; d, caudal to coronoid process [a/0 b/1 c/2 d/3]

32 **MA7** Mandibular symphysis: a, very short; b, not short [a/0 b/1]

33 **MA8** Rami, in dorsal view: a, bowed laterad, then sharply mediad rostrally; b, straight; c, with definite angle [a/0 b/1 c/2]

34 **MA9** Retroarticular process: a, absent; b, small; c, large [a/0 b/1 c/2]

35 **MA10** Dorsal edge of rami: a, turned over laterally to form a flange; b, no flange [a/0 b/1]

36 **MA11** Tip: a, pointed; b, blunt or rounded [a/0 b/1]

37 **MA12** Symphysis: a, excavated into U-shape; b, filled to a flat surface [a/0 b/1]

38 **FU1** Head of clavicle: a, attenuated, pointed caudally; b, terminating more or less acutely, but not pointed [a/0 b/1]

39 FU2 Coracoid articular surface: a, raised from blade dorsally and ventrally; b, not raised; c, raised ventrally; d, raised dorsally

40 **FU3** Hypocleidium: a, present; b, absent [a/0 b/1]

41 FU4 Axis of coracoidal articulation: a, in line with caudal margin of furcula at ventral end of articulation: b, at angle of less than 90°; c, at c.90° [a/0 b/1 c/2]

42 FU5 Length of coracoid articular facet: a, about equal to ramal width; b, up to two-thirds ramal width [a/0 b/1]

43 FU6 Rami bent: a, once, near dorsal end; b, once, near the centre; c, twice, dorsally and ventrally [a/0 b/1 c/2]

44 FU7 Pneumatic foramina in lateral fossa with: a, absent; b, present [a/0 b/1]

45 FU8 Dorsocaudal tip of furcula: a, in contact with acromion; b, not in contact [a/0 b/1]

46 ST1 Coracoidal sulci: a, separated at manubrial spine; b, closely adjacent; c, overlapping [a/0 b/1 c/2]

47 ST2 Number of rib articulations on costal margin: a, 4; b, 5; c, 6; d, 7 [a/0 b/1 c/2 d/3]

48 ST3 Sternocoracoidal impression: a, with pneumatic fossa; b, without foramen [a/0 b/1]

49 ST4 Tubercle for brace ligament: a, present; b, absent [a/0 b/1]

50 ST5 Caudal margin: a, thickened, triangular in outline; b, bluntly pointed; c, almost square, slightly indented, or notched; d, deeply square-notched, leaving acute triangle medially [a/0 b/1 c/2 d/3]

51 ST6 Sternocoracoidal fossa extending caudally to: a, 2nd costal articulation; b, 3rd articulation; c, 4th articulation; d, 5th articulation; e, 6th or 7th [a/0 b/1 c/2 d/3 e/4]

52 ST7 Sternocoracoidal process: a, with anteromedial projection; b, with no projection [a/0 b/1]

53 ST8 Lateral processes: a, present; b, rudimentary; c, absent [a/0 b/1 c/2]

54 ST9 Ventral margin of sternocoracoidal fossa: a, adjacent to M. supracoracoideus scar; b, well separated from scar [a/0 b/1]

55 ST10 Manubrial spine: a, short, blunt; b, long, thin [a/0 b/1]

56 ST11 Scar of M. supracoracoideus: a, lobed; b, with smoothly curved outline [a/0 b/1]

57 ST12 Cranial end of sternal carina: below base of manubrial spine; b, caudal to base of manubrial spine; c, well cranial to base of spine (below spine tip) [a/0 b/1 c/2]

58 ST12A Deepest point of sternal carina: a, at cranial end; b, displaced caudad [a/0 b/1]

59 CO1 Clavicular facet in medial view: a, divided into cranial and caudal sections by shallow depression; b, a single, well-defined facet ending ventrally in sharp, projecting line; c, a separate facet on the ventrolateral surface [a/0 b/1 c/2]

60 CO2 Distinct facet on dorsal surface between lateral margin and sternocoracoidal impression: a, present; b, absent [a/0 b/1]

61 CO3 Sternocoracoidal tuberosity (posterior ligament scar): a, prominent; b, obscure; c, absent [a/0 b/1 c/2]

62 CO4 Oval or circular impression on dorsolateral surface opposite coracoidal fenestra: a, distinct; b, obscure; c, absent; d, present, proximal to coracoidal fenestra [a/0 b/1 c/2 d/3]

63 CO4A (**CO20**) Coracoidal fenestra: a, always present; b, variable; c, absent [a/0 b/1 c/2]

64 CO5 Dorsolateral surface of head: a, with distinct fossa; b, without fossa [a/0 b/1]

65 CO6 Subclavicular fossa: a, with pneumatic foramen (-ina); without foramen (-ina) [a/0 b/1]

66 CO7 Tip of procoracoid: a, deflected ventrad; b, not deflected [a/0 b/1]

67 CO8 Sternocoracoidal process: a, short, with parallel sides [a/0 b/1 c/2 d/3]

68 CO9 Insertion of posterior ligament: a, lateral; b, near sternocoracoidal impression; c, medial; d, on coracoid shaft [a/0 b/1 c/2 d/3]

69 CO10 Sternocoracoidal impression: a, without pneumatic foramina; b, without foramina [a/0 b/1]

70 **HU1** Brachial impression: a, extending as deep pit between proximal edges of internal and external condyles; b, not extending between condyles as pit [a/0 b/1]

71 **HU2** Outline of proximal margin of deltoid crest: a, concave; b, straight; c, convex [a/0 b/1 c/2]

72 **HU2A** Distal end of deltoid crest: a, running smoothly into line of shaft (except for pectoral attachment tubercle); b, with a distinct step to shaft [a/0 b/1]

73 HU2B Apical 'crestlet' on deltoid crest: a, present; b, absent [a/0 b/1]

74 HU2C External tuberosity: a, on line between deltoid crest and head; b, cranial to axis of head [a/0 b/1]

75 **HU2D** Proportions of deltoid crest: a, proximal section shorter than distal; b, proximal section longer than distal; c, sections of equal length [a/0 b/1 c/2]

76 **HU2E** Outline of distal margin of deltoid crest: a, concave; b, straight; c, convex [a/0 b/1 c/2]

77 **HU3** Position of nutrient firamen with respect to distal end of bicipital crest: a, opposite; b, distal to; c, well distal to; d, at c. 50 % of shaft [a/0 b/1 c/2 d/3]

78 **HU4** Position of nutrient foramen with respect to distal end of deltoid crest: a, opposite; b, proximal to; c, distal to crest [a/0 b/1 c/2]

79 **HU5** Ligamental groove: a, entire, deep, cutting off bicipital surface; b, shallow, rectangular [a/0 b/1]

80 **HU6** Bicipital furrow: a, deep, narrow; b, broad; c, obscure to obsolete [a/0 b/1 c/2]

81 **HU7** Shape of bicipital surface in internal view: a, convex, evenly rounded from bicipital crest; b, flat, with small radius curve from bicipital crest; c, concave [a/0 b/1 c/2]

82 HU8 Orientation of proximal margin of internal tuberosity: a, proximad; b, distad [a/0 b/1]

83 **HU9** Distal extension of median crest: a, running into margo caudalis (caudal margin); b, parallel to caudal margin; c, parallel to caudal margin, but with deep fossa between [a/0 b/1 c/2]

84 **HU10** Orientation of bicipital crest to shaft, at distal end of crest: a, meeting shaft at ± 90°; b, at acute angle; c, running into line of shaft [a/0 b/1 c/2]

85 **HU11A** Outline of internal margin of bicipital crest viewed normal to shaft: a, with definite angle proximally and distally, ± parallel to shaft between; b, ± evenly curved; c, with definite proximal and distal angles and internal margin diverging internally proximally; d, with angle to shaft distally, parallel to shaft on to internal tuberosity proximally; e, as in d but angled towards shaft proximally; f, a single angle [a/0 b/1 c/2 d/3 e/4 f/5]

86 HU12 Proportion of pneumatic fossa occupied by pneumatic foramen: a, most (>⅔); b, part (<⅔) [a/0 b/1]

87 HU13 Internal tricipital groove: a, deep, with sharp external ridge; b, shallow to obscure [a/0 b/1]

88 **HU13A** Distal anconal fossa: a, triangular section, with internal side deepest; b, rectangular section; c, divided by strong external margin to inner tricipital groove [a/0 b/1 c/2]

89 **HU14** Distal end of bicipital crest: a, a wide shelf; b, narrow shelf; c, no shelf [a/0 b/1 c/2]

90 HU15 Attachment of infraspinatus on proximal bicipital crest: a, elongate; b, short, rounded [a/0 b/1]

91 HU16 Attachment of supraspinatus: a, clear, raised; b, inconspicuous [a/0 b/1]

92 HU17 Extent of external tuberosity in palmar view: a, prominent; b, in line from head to deltoid crest [a/0 b/1]

93 HU18 Impression of brachialis anticus in brachial depression: a, an extended pit; b, a raised scar; c, extending proximally from brachial depression [a/0 b/1 c/2]

94 HU19 Bicipital crest: a, thick; b, thin [a/0 b/1]

95 HU20 Shaft anconal to ectepicondylar prominence: a, with fossa; b, without fossa, shaft smoothly convex [a/0 b/1]

96 **HU21** Shape of apex of deltoid crest: a, angular, 'sharp'; b, smoothly rounded [a/0 b/1]

97 HU22 Ectepicondylar prominence: a, blunt, with or without distinct pit; b, pointed [a/0 b/1]

98 HU23 Position of deltoid crest apex: a, opposite distal end of bicipital crest; b, distal to distal end of bicipital crest [a/0 b/1]

99 **HU24** Bicipital crest terminating as: a, sharp ridge along internal margin; b, ridge cranial to internal margin; c, very short ridge [a/0 b/1 c/2]

100 **HU25** Distal end of median crest: a, proximal to distal end of bicipital crest; b, opposite distal end of bicipital crest [a/0 b/1]

101 **HU26** Brachial depression: a, deep; b, shallow [a/0 b/1]

102 **HU27** Lateral extent of ectepicondylar prominence in anconal view: a, projecting beyond external margin as strong ridge; b, not projecting beyond margin as ridge [a/0 b/1]

103 HU28 Impressions of Mm. latissimus dorsi: a, in shallow groove; b, not in groove [a/0 b/1]

104 **HU29** Distal margin of bicipital surface delimited by: a, wide notch; b, faint groove, no notch; c, definite groove, but no notch; d, step [a/0 b/1 c/2 d/3]

105 HU30 'Swelling' below head, at distal end of capital groove: a, present to well-developed; b, absent; c, pit, not a swelling [a/0 b/1 c/2]

106 **HU31** Shape of external tricipital groove: a, shallow or indistinct; b, deep, with raised internal border [a/0 b/1]

107 **HU32** Caudal margin: a, rounded; b, an angle defined by planes above and below; c, as in b, but sharp angle of c. 90° [a/0 b/1 c/2]

108 **UL1** Shape of distal end of brachialis anticus impression: a, acute; b, rounded [a/0 b/1]

109 **UL2** Shaft proximal to trochlea: a, trochlea undercut by fossa; b, deep fossa, but not undercutting trochlea; c, fossa shallow or obscure [a/0 b/1 c/2]

110 UL3 Intermuscular line past nutrient foramen: a, sharp; b, obscure or absent [a/0 b/1]

111 **UL3A** 'Double' intermuscular line: a, reaching, or nearly so, nutrient foramen; b, merging well proximal to foramen; c, merging distal to foramen; d, single throughout length [a/0 b/1 c/2 d/3]

112 **UL4** Proximal end of brachialis anticus impression: a, with pneumatic foramina; b, not pneumatic [a/0 b/1]

113 **UL5** Junction between internal margin of shaft and external condyle: a, smooth; b, with pronounced step [a/0 b/1]

114 UL6 Carpal tuberosity: a, bluntly pointed; b, 'squared off' [a/0 b/1]

115 **UL7** Proximal end of brachialis anticus impression: a, broad, shallow; b, deep groove, with internal border extended as thin shelf; c, narrow; prominence for anterior articular ligament broad [a/0 b/1 c/2]

116 UL8 Olecranon: a, acutely pointed; b, blunt [[a/0 b/1]

117 **UL9** Outline of external condyle: a, evenly rounded; b, with distal angle = 'squared' [a/0 b/1]

118 UL10 Process beside distal tendinal pit: a, prominent; b, obscure [a/0 b/1]

119 **UL11** Position of nutrient foramen relative to brachialis anticus impression: a, less than length of impression distal to impression; b, about length of impression distal to impression; c, further distal to impression than length of impression [a/0 b/1 c/2]

120 **UL12** Proximal surface of carpal tuberosity: a, undercut by fossa; b, not undercut [a/0 b/1]

121 **UL13** Proximal margin of trochlea: a, angular, with sharp internal angle at junction with internal condyle; b, smooth curve [a/0 b/1]

122 UL14 Orientation of axis of carpal tuberosity: a, proximad; b, distad [a/0 b/1]

123 **CM1** Proximal internal edge of minor metacarpal: a, with prominent, flat-ended tubercle; b, no tubercle, perhaps a rounded swelling [a/0 b/1]

124 CM2 Pisiform process: a, thin, rounded in section; b, long, oval or rectangular in section; c, robust, round [a/0 b/1 c/2]

125 **CM3** Pollical facet: a, rounded; b, proximal and distal notches dividing surface into two segments; c, surfaces separated; d, notched, internal surface reduced [a/0 b/1 c/2 d/3]

126 **CM4** Depressio metacarpi interna: a, shallow; b, deep [a/0 b/1]

127 CM5 Sulcus internus: a, deep, internal surface of major metacarpal rounded, distal symphysis projecting internally; b, broad and shallow, internal surface of major metacarpal flattened, symphysis not projecting [a/0 b/1]

128 **CM6** Depressio metacarpi externa: a, deep; b, shallow [a/0 b/1]

129 **CM7** Shape of carpal trochlea in proximal view: a, internal condyle concave internally; b, concave externally [a/0 b/1]

130 **CM7A** Shape of carpal trochlea in proximal view: a, external condyle concave internally; b, external condyle concave externally; c, straight [a/0 b/1 c/2]

131 **CM7B** Junction of proximal end of external margin of minor metacarpal: a, in line with external condyle; b, in line with internal condyle; c, between condyles [a/0 b/1 c/2]

132 **CM7C** Proximal end of minor metacarpal: a, with deep fossa; b, with no fossa; c, with shallow groove [a/0 b/1 c/2]

133 **CM8** Posterior carpal fossa: a, deep; b, shallow [a/0 b/1]

134 CM9 Ligamental attachment of pisiform process: a, prominent swelling, with or without pit; b, small or obscure [a/0 b/1]

135 **CM10** Position of pollical facet: a, less than or equal to 50% of distance from internal condyle to distal end of proximal symphysis; b, more than 50% to distal end of proximal symphysis [a/0 b/1]

136 **CM11** Length of distal symphysis: a, less than or equal to distal width of major metacarpal; b, greater than width of major metacarpal [a/0 b/1]

137 **CM12** Anterior carpal fossa: a, shallow; b, deep pit; c, pit, with pneumatic foramen or foramina [a/0 b/1 c/2]

138 **CM13** Internal ligamental fossa: a, shallow; b, deep [a/0 b/1]

139 **CM14** Junction of distal end of internal of condyle with shaft: a, smooth; b, stepped [a/0 b/1]

140 CM15 Shape of end of major metacarpal in distal view: a, approximately rectangular; b, more or less triangular, anteroexternal side convex [a/0 b/1]

141 **CM16** Facet for digit of minor metacarpal: a, set off from major metacarpal by deep pit; b, no deep pit [a/0 b/1]

142 **PE1** Dorsal fenestrae: a, large, conspicuous; b, absent or small [a/0 b/1]

143 **PE2** Postacetabular ilium and synsacral plate: a, fused, with no obvious suture; b, not fused [a/0 b/1]

144 **PE3** Cranial ends of iliac plates: a, rounded in dorsal view; b, straight or inclined anterolaterally [a/0 b/1]

145 **PE4** Posterior iliac crests: a, more or less straight and parallel; b, bowed outward [a/0 b/1]

146 **PE5** Width across posterior iliac crests in dorsal view: a, about equal to pelvis length; b, less than two-thirds pelvis length [[a/0 b/1]

147 **PE6** Anterior iliac crests: a, separated from synsacral plate by large fenestrae (technical term available); b, not separated [a/0 b/1]

148 **PE7** Posterior iliac crests: a, produced as square process above acetabulum; b, produced above acetabulum, but not forming square process; c, not produced above acetabulum [a/0 b/1 c/2]

149 **PE8** Shape of posterior end of ilioischiadic plate: a, tapering to rounded point; b, notched; c, abruptly arrowing before posterior extremity; d, knickpoint in posterior iliac crest [a/0 b/1 c/2 d/3]

150 **PE9** Pubis: a, rodlike, not expanded; b, slight expansion; c, with broad expansion [a/0 b/1 c/2]

151 **PE10** Shape and direction of anterior synsacral caudal vertebrae: a, long, slender, parallel, or diverging towards acetabulum; b, relatively short, broadly converging [a/0 b/1]

152 **PE11** Posterior synsacral caudal vertebrae: coalescing with broad, medially projecting plate; b, free, articulating with mesial iliac edge (Note: In Sagittarius there is a broad plate enclosing the posterior ilioischiatic space ventrally) [a/0 b/1]

153 **PE12** Number and arrangement of caudal synsacral vertebrae (anterior, posterior): a, 2+2; b, 2+3; c, 2+2+1; d, 3+3; e, 2+3+1 [a/0 b/1 c/2 d/3 e/4]

154 **PE13** Posterior iliac crests above ilioischiatic fossa: a, shelf-like; b, not produced as a shelf [a/0 b/1]

155 PE14 Mesial protuberance at posterior ilio-ischiatic suture: present, forming 'constriction' of cauadal space; b, absent [a/0 b/1]

156 **FE1** Rotular groove: a, in line with shaft; b, at angle to shaft [a/0 b/1]

157 **FE2** Rotular groove: a, short; b, long [a/0 b/1]

158 **FE3** Pneumatic foramen: a, absent; b, present [a/0 b/1]

159 **FE4** Cranial outline of shaft: a, straight in lateral view; b, curved in lateral view; b, bent caudad near distal end; c, bent caudad near midpoint of shaft [a/0 b/1 b-c/2 c/3 c-a/4]

160 **FE5** Trochanteral ridge: a, short cranially, but extending proximoplantad as strong ridge; b, not so [a/0 b/1]

161 **FE6** Cranial intermuscular line(s): a, medial; b, lateral;, c, along centre-line [a/0 a-b/1 b/2 c/3 c-a/4]

162 **FE7** Number of cranial intermuscular lines: a, 1; b, 2 [a/0 b/1]

163 **FE8** Medial condyle: a, projecting in line with shaft; b, projecting cranially [a/0 b/1]

164 **FE9** Popliteal fossa: a, deep; b, shallow and broad; c, shallow, with deep pit; d, narrow, aligned with shaft; e, undercutting condyles [a/0 b/1 c/2 d/3 e/4]

165 **FE10** Popliteal fossa: a, with pneumatic foramen; b, without [a/0 b/1]

166 **FE11** Caudal intermuscular line: a, single, weakly defined; b, forked; c, strongly defined, central on shaft; d, multiple [a/0 b/1 c/2 d/3]

167 **FE12** Rotular groove section: a, rectangular; b, U-shaped; c, approximately V-shaped [a/0 a-b/1 b/2 b-c/3 c/4]

168 **FE13** Large muscle scar proximal to popliteal fossa: a, a line; b, more or less oval; c, divided into 2 separate scars [a/0 a-b/1 b/2 c/3]

169 **FE13A** Large muscle scar proximal to popliteal fossa: a, central on caudal surface; b, lateral; c, medial [a/0 a-b/1 b/2 b-c/3 c/4]

170 **FE13B** Large muscle scar proximal to popliteal fossa: a, a pit; b, a tubercle [a/0 b/1]

171 **FE14** Caudal intercondylar notch: a, V-shaped; b, deep U-section completely separating surfaces so that inner face of condyle is equal to outer face height; c, shallow U-section [a/0 b/1 c/2]

172 **FE15** Proximal caudal fossa: a, deep; b, shallow; c, shaft convex [a/0 a-b/1 b/2 c/3]

173 **FE16** Caudal edge of iliac surface: a, smoothly curved; b, with distinct angle [a/0 a-b/1 b/2]

174 **FE17** Shallow secondary fossa proximal to popliteal fossa: a, present; b, absent [a/0 b/1]

175 **FE18** Median face of median condyle: a, with fossa; b, without fossa (perhaps small pit); c, with large tubercle [a/0 b/1 c/2 a-c/3]

176 **FE19** Transition of proximal cranial end of median condyle with shaft: a, stepped; b, smooth; c, a high step [a/0 a-b/1 b/2 b-c/3 c/4 a-c/5]

177 **FE20** Cranial ridge of median condyle: a, extending further proximally than lateral ridge; b, equal; c, lateral extending further proximally [a/0 b/1 c/2]

178 **FE21** Fibular condyle: a, narrow; b, shelf-like; c, with deep pit proximally [a/0 b/1 c/2]

179 **FE22** Proximal edge of fibular condyle: a, with muscle insertion pit running distally as large notch, so that outline of condyle is a blunt projection; b, partly notched; c, square; d, not notched, rounded; e, not notched, but with a large pit; f, not notched, with the proximal outline square [a/0 b/1 c/2 d/3 e/4 f/5]

180 **FE23** Prominent tubercle on medial margin distal to femur head: a, present; b, absent; c, a raised linear scar [a/0 b/1 c/2]

181 **FE24** Trochanteral ridge: a, high, so that proximal outline of bone nearly triangular; b, low, outline of bone ± rectangular [a/0 b/1]

182 **FE25** Median condyle: a, ± flat in distal view, from intercondylar notch to median margin; b, curved; c, with definite angle; d, concave [a/0 a-b/1 b/2 b-c/3 c/4 d/5 a-d/6]

183 **FE26** Proximo-lateral extension of fibular condyle: a, absent; b, pointed; c, ± square; d, rounded; e, double [a/0 a-b/1 b/2 b-c/3 c/4 a-c/5 d/6 e/7]

184 **FE25** Median condyle: a, square; d, rounded; e, double [a/0 a-b/1 b/2 b-c/3 c/4 a-c/5 d/6 e/7]

184 **FE27** Prominent tubercle medial to popliteal fossa: a, present; b, absent [a/0 b/1]

185 **FE28** Proximal trochanteral ridge turned medially to overhang and form fossa on and above iliac surface: a, present; b, absent; c, with second fossa [a/o b/1 a-c/2 b-c/3 c/4]

186 **FE29** Cranial intermuscular line: a, nearly straight; b, directed toward lateral margin, then straight down shaft, forming clear angle [a/0 b/1]

187 **FE30** Caudal junction of medial condyle with shaft: a, with tubercle; b, tubercle extending laterally as ridge (forming pit); c, tubercle small to absent; d, tubercle extending proximo-laterally as line towards scar of FE13 [a/0 b/1 c/2 d/3]

188 **FE31** Proximal outline of trochanteral ridge in lateral view: a, angular, with distal limb returned; b, rounded; c, angular [a/0 b/1 c/2]

189 **FE32** Cranial edge of iliac facet: a, a slight crest; b, not a crest [a/0 a-b/1 b/2]

190 **FE33** Proximal end of lateral condyle; muscle insertion at proximal end of ridge: a, at junction with shaft (termination coincides with shaft margin); b, displaced laterally [a/0 b/1]

191 **FE34** Bone proportions: a, long and slender; b, of 'normal' proportions [a/0 b/1]

192 **FE35** Prominent muscle attachment across popliteal fossa: a, a line; b, absent [a/0 b/1]

193 **FE36** Muscle scar of 13A and B: a, distal to or ± in popliteal fossa; proximal to fossa [a/0 b/1]

194 **FE37** Depth of rotular groove: a, equal to depth; b, less than width; c, much less than width [a/0 a-b/1 b/2 b-c/3 c/4]

195 **FE38** Trochanteral ridge: a, ± smoothly curved over pneumatic foramen in lateral view; b, arched over foramen; c, with a large swelling distal to foramen; d, with a very large muscle scar distally [a/0 a-b/1 b/2 b-c/3 a-c/4 c/5 d/6]

196 **FE39** Area proximal to pneumatic foramen: a, with no ridge; b, with strong transverse ridge; c, with trochanter medial enough for intermuscular line to run distad down medial side of foramen directly from it [a/0 b/1 c/2]

197 **FE40** Distal part of external face of fibular condyle: a, impressed so that proximo-lateral process stands proud of lateral surface; b, not impressed [a/0 b/1]

198 **FE41** Proximo-caudal median protuberance: a, absent; b, present [a/0 b/1]

199 **FE42** Trochanteral ridge and lateral margin of iliac facet: a, merged cranially; b, separated [a/0 b/1]

200 **FE43** Proximal cranial end of lateral condyle: a, with no step; with obvious step [a/0 b/1]

201 **TI1** Distal condyles: a, extending as far caudally as cranially; b, ± in line with posterior surface of shaft [a/0 b/1]

202 **TI2** Trocheal groove and sulcus: a, very deep; b, shallow [a/0 b/1]

203 **TI3** Sulcus: a, caudal to line of shaft; b, running into caudal surface [a/0 b/1]

204 **TI4** Fibula insertion: a, near distal end of shaft; b, 0.5-0.67 distance down shaft [a/0 a-c/1 b/2 b-c/3 c/4]

205 **TI5** Lateral cnemial crest: a, long (> width); b, short (= width) [a/0 b/1]

206 **TI6** Medial proximal ligaments: a, inserting on shaft midline; b, inserting at distal end of medial crest [a/0 a-b/1 b/2]

207 **TI7** Lateral proximal articular surface: a, deeply excavated; b, not deeply excavated, or pit laterally [a/0 b/1]

208 **TI8** Proximal plantar surface: a, strongly keeled (with lateral and/or medial fossae); b, rounded; c, low keel or ridge, not defined by fossae [a/0 a-c/1 b/2 b-c/3 c/4]

209 **TI9** Lateral cranial fossa: a, open to head; b, filled to distal edge of ridge running from lateral crest [a/0 b/1]

210 **TI10** Median cnemial crest: a, notched; b, smoothly convex; c, short, ≥ lateral length, with sharp angle separating proximal from distal sections; d, stepped at distal end [a/0 a-b/1 a-c/3 b/4 b-d/5 c/6 d/7]

211 **TI11** Sulcus extending: a, ± equally op cranial and caudal surfaces; b, ≥ 50% higher up caudal surface [a/0 b/1]

212 **TI12** Condyles: a, equal in width; b, medial condyle wider; c, lateral wider [a/0 b/1 c/2]

213 **TI13** Lateral condyle caudal limb: a, entire; b, notched [a/0 b/1]

214 **TI14** Distal margins of shaft: a, diverging abruptly to width over condyles; b, subparallel near condyles [a/0 b/1]

215 **TI15** Supratendinal bridge: a, 30-60° to shaft axis; b, ± at right angles to axis; c, ± parallel to axis [a/0 a-b/1 a-c/2 b/3 c/4]

216 **TI16** Muscle scar: a, at proximal end of supratendinal bridge; b, proximal to proximal end; c, well proximal to end; d, on medial margin [a/0 a-b/1 b/2 b-c/3 c/4 d/5]

217 **TI17** Muscle scar: a, a surface roughening; b, a prominent tubercle; c, a pit [a/0 b/1 c/2]

218 **TI18** Intercondylar groove: a, narrow; b, broad; c, shallow or obscure [a/0 b/1 c/2]

219 **TI19** Tibial cartilage sulcus: a, tapering; b, ± parallel-sided [a/0 b/1]

220 **TI20** Caudal arm of medial condyle: a, entire; b, notched [a/0 b/1]

221 **TI21** Cranial proximal sulcus: a, excavated; b, obscure [a/0 b/1]

222 **TI22** Medial shaft margin opposite supratendinal bridge: a, convex; b, concave; c, straight [a/0 b/1 c/2]

223 **TI23** Supratendinal bridge: a, narrow (length > width); b, broad (length ≥ width); c, length >> width [a/0 b/1 c/2]

224 **TI24** Supratendinal bridge: a, flat; b, twisted; c, round; d, bent [a/0 b/1 d/2]

225 **TI25** Supratendinal bridge: a, narrowing distally; b, parallel-sided; c, narrowing proximally; d, narrowing proximally and distally; e, narrowing centrally, pinched [a/0 a-c/1 b/2 c/3 d/4 e/5]

226 **TI26** Supratendinal bridge arising: a, away from medial margin; b, from medial margin [a/0 a-b/1 b/2]

227 **TI27** Distal tendinal bridge orifice: a, circular; b, subtriangular [a/0 a-b/1 b/2]
228 **TI28** Lateral condyle: a, squared off proximally; b, tapering proximally [a/0 b/1]
229 **TI29** Proximal cranial end of medial condyle: a, squared off; b, extending laterally to partly obscure distal orifice of tendinal canal; c, tapering proximally [a/0 a-b/1 b/2 c/3]
230 **TI30** Nutrient foramen: a, proximal to distal end of fibular crest; b, opposite end of crest; c, distal to end of crest [a/0 b/1 c/2]
231 **TI31** Entepicondylar prominence: a, very small to absent; b, small; c, large [a/0 a-b/1 b/2 b-c/3 c/4]
232 **TI32** External ligamental attachment: a, very small to absent; b, triangular; c, shelf-like; d, on lateral condyle; e, a lateral tubercle; f, a ridge [a/0 a-b/1 b/2 c/3 c-f/4 d/5 e/6 f/7]
233 **TI33** Surface distolateral to tendinal canal: a, broad; b, narrow [a/0 b/1]
234 **TI34** Surface distolateral to tendinal canal: a, without prominence or pit; b, with prominence; c, with pit; d, with deep, narrow pit [a/0 b/1 b-c/2 c/3]
235 **TI35** Tendinal canal: a, central on shaft; b, confined to medial side of centre line; c, extending across most of shaft, deep and sunken [a/0 a-b/1 a-c/2 b/3 c/4]
236 **TI36** Medial margin at tendinal canal: a, broad; b, a thin plate [a/0 a-b/1 b/2]
237 **TI37** Median condyle: a, recurved proximo-cranially; b, not recurved; c, with no sharp angle, running smoothly from shaft [a/0 b/1 c/2]
238 **TI38** Medial distal caudal groove: a, convex or flat, edge not extending medially; b, deeply concave, edge extending medially [a/0 b/1]
239 **TI39** Medial distal caudal groove: a, without proximal pit; b, with proximal pit [a/0 b/1]
240 **TI40** Cranial surface of median condyle: a, not inflated; b, inflated [a/0 b/1]
241 **TI41** Proximal cranial sulcus: a, narrow (≤ 50% of cranial surface); b, wide [a/0 b/1] (refers to position of lateral crest)
242 **TI42** Ectepicondylar prominence: a, absent; b, small; c, large; d, linear [a/0 a-b/1 b/2 b-c/3 b-d/4 c/5 d/6]
243 **TI43** Medial condyle: a, entire in distal view; b, notched [a/0 a-b/1 b/2]
244 **TI44** Intercondylar space: a, narrow (< condyle width); b, wide (> condyle width); c, equal to condyle width [a/0 a-c/1 b/2 b-c/3 c/4]
245 TM1 Calcaneal processes: a, widely separated; b, close-set
246 **TM2** Tendinal canal: a, open; b, almost closed; c, closed [a/0 b/1 c/2]
247 TM3 Outer calcaneal process: a, produced, almost as large as inner; b, displaced laterally and flattened; c, otherwise
248 **TM4** Notch for peronaeus nerve: a, absent; b, indistinct; c, wide-mouthed; d, almost closed (270° closure) [a/0 b/1 c/2 d/3]

249 **TM5** Lateral calcaneal ridge: a, extending distally, fading into lateral posterior margin; b, delineated medially by fossa of abductor digiti IV muscle; c, lateral ridge displaced medially and fused with medial ridge; d, displaced medially but not fused; e, lacking, posterior aspect ± flat, ridge a line marking margins of abductor digiti IV and adductor digiti II impressions [a/3 b/4 c/0 d/1 e/2]

250 **TM6** Median calcaneal process: a, pillar-like; b, an elongated plate; c, otherwise [a/0 b/1]

251 TM7 Proximal and posterior margins of median calcaneal process: a, bent medially; b, not bent medially

252 TM8 Medial calcaneal process: a, separated from medial margin by fossa of flexor hallucis brevis; b, lacking distinct fossa medial to process, which arises almost from margin of bone

253 **TM9** Medial proximal vascular foramen: a, medial and proximal to distal margin of medial process; b, medial to distal margin or on ridge below distal margin; c, lateral to ridge; d, on ridge below distal margin to just lateral to margin [a/0 a-b/1 b/2 b-c/3]

254 TM10 Tubercle for tibialis anticus: a, lateral to midline; b, just medial to midline

255 TM11 Lateral proximal vascular foramen: a, on medial side of lateral ridge; b, on lateral side or on lateral slope of hypotarsal ridge

256 TM12 Lateral condylar surface: a, higher than medial; b, surfaces at equal level, or medial higher

257 TM13 Tibialis anticus tubercle: a, near proximal foramina; b, not near foramina

258 TM14 Lateral metatarsal prominence: a, hardly discernible; b, well-defined

259 TM15 Frenula: a, completely ossified; b, present; c, absent [It should be possible to sub-divide b: scars project, narrowly separated, near medial margin; broad lateral scar nearly on mid-line; scars at different levels, medial higher than lateral; lateral higher than medial; at same level]

260 TM16 Posterior flexor groove: a, hollowed out and unmarked; b, relatively flat, with a series of shallow impressions for 3 posterior muscles

261 TM17 Scar of first metatarsal: a, directed ± medially; b, directed posteriorly

262 TM18 Proximal edge of metatarsal facet: a, raised, separated from projecting line of medial tarsal edge by notch; b, not separated by notch

263 TM19 Openings at distal end end of tendinal groove: a, two; b, one

264 TM20 Extensor digiti III origin's upper and medial margins: a, indicated by scar; b, not indicated by scar

265 TM21 Cranial surface proximal to middle trochlea: a, with pit; b, no pit; c, indistinct pit

266 TM22 Origin of abductor digiti II: a, fairly distinct, roughened, extending from tibilalis anticus to upper and lateral margins of first metatarsal articulation; b, not so

267 TM23 Inner trochlea (digit II) posteromedial process: a, bent toward tarsal midline; b, not bent

268 TM24 Posterolateral process of digit II trochlea: a, short, thick, separated from articular surface by groove; b, not so

269 TM25 Digit IV trochlea posterolateral projection margin: a, truncated, pointed at ventroposterior angle; b, rounded posteriorly

270 TM26 Groove for abductor digiti IV tendon on posterolateral margin of shaft: a, wide, clearly marked; b, narrow, shallow

270 TM27 Proximal anterior fossa: a, deep; b, shallow

271 **PH1** Phalanges 1 and 2 on pedal digit 2: a, free; b, fused in most or all specimens [a/0 b/1]

272 **PX1** Number of cervical vertebrae: a, 13; b, 14; c, 15; d, 17 [a/0 b/1 c/2 d/3]

273 **PX2** Number of cervical ribs: a, 1; b, 2; c, 3 [a/0 b/1 c/2]

Appendix 5.2 Characters states for taxa included in phylogenetic analysis. See Appendix 5.1 for descriptions of characters and codes. Taxa by genus name or first eight letters of generic name.

Node	CC CCCRRM RRR11A 234781	MMMMMM AAAAAA 234567	MMM MMAAAP AA111H 890121	C PPOFFH XX2UUU 120131	HHH HUUUHH U222UU 2ADE34	HU HHHHU1 UUUU11 56790A	H UHH 1UU 312 A41
1 SAGITTAR	0?0?21	1110?1	001000	21????	100122	112114	011
2 PANDION	??0??0	101121	100000	21?000	002221	000202	101
3 ELANOIDE	400001	110001	000000	110101	101211	022113	001
4 PERNIS	200001	210111	200100	210101	102211	111101	000
5 MACHAERH	?00021	101110	020000	110101	012111	000211	010
6 ELANUS	201001	111120	010000	110111	0??220	000011	200
7 ICTINIA	000001	100111	100101	220111	011011	120121	010
8 MILVUS	000001	112311	010101	110111	112111	000213	000
9 HALIASTU	?00001	111111	120101	??0111	012121	122113	000
10 HALIAEET	100011	100321	101101	110111	212020	110211	000
11 ICHTHYOP	?00021	100321	111101	??011?	??????	??????	???
12 GYPOHIER	?00021	110111	111000	210111	012121	111203	001
13 NEOPHRON	200021	300331	111000	110111	102211	111110	101
14 GYPAETUS	?00001	111130	001100	210111	202011	21111?	001
15 NECROSYR	?00001	311101	121100	210111	102121	222111	011
16 GYPS	200001	102001	110100	310111	200132	222104	100
17 AEGYPIUS	200001	100001	110100	210111	202221	222104	000
18 CIRCAETU	200001	101321	120000	??0111	210221	120214	001
19 TERATHOP	?00001	112321	010100	210111	112011	122121	011
20 SPILORNI	?00001	102321	120000	110111	212221	121100	000
21 POLYBORO	200001	112111	110000	100111	112211	211121	111
22 CIRCUS	?00101	100121	020110	??1111	110201	210221	010
23 MELIERAX	?00001	110111	110100	??0111	010221	110121	010
24 ERYTHROT	?0000?	??????	??????	??1111	012221	111200	000
25 ACCIPITE	000001	110310	120100	??2111	012121	010100	101
26 KAUPIFAL	?00001	110211	110000	??0111	012221	210211	000
27 LEUCOPTE	000001	100331	110000	??0111	010211	011210	111
28 BUTEOGAL	000001	111111	110000	??0111	112111	211221	120
29 HETEROSP	000001	112211	010000	??0111	112111	111121	110
30 BUSARELL	000001	112111	110001	??0111	000021	111120	111
31 GERANOAE	?00001	1110?0	010000	??0111	110111	012213	010
32 BUTEO	100001	112311	020000	110111	212220	111200	100
33 PARABUTE	?00001	100311	120000	??0111	212211	111211	110
34 MORPHNUS	?0000?	??????	?????0	??0111	210121	200213	010
35 HARPIA	?00001	102311	020100	210111	110011	111211	010
36 PITHECOP	?00001	112111	110100	110111	202011	122225	111
37 AQUILA	300011	101111	110100	110111	211121	211111	010
38 HIERAAET	?00001	101311	110100	??0111	211121	111110	000
39 LOPHAETU	?00001	111111	000000	??0111	012120	111110	100
40 SPIZAETU	?00001	112221	120100	??0111	012221	110115	111
41 STEPHANO	?00001	102311	101100	??0111	212020	210111	010
42 POLEMAET	?00001	110311	100100	??0111	210111	122113	010
43 GERANOSP	?00001	111131	010000	??0111	002121	110115	020
44 HARPAGUS	?00001	012121	000100	??1111	202121	101011	110
45 HARPAGOR	2?0001	112311	121100	??0101	212121	121114	100

Appendix 5.2 (continued)

Node	HHHHHH UUUUUU 222223 456791	H U UUULUU 3LL3LL 212A45	UUU UULLLC LL111M 791231	CC CCCCMM MMMM77 3467AB	C CCCC MCMMMM 7M1111 C80123	CC MMSSSP 11TTTE 461231	PPP EEE 234
1 SAGITTAR	210001	002111	202111	010000	201100	110101	000
2 PANDION	010011	101110	202111	300100	100011	00?211	111
3 ELANOIDE	100011	102210	110100	110111	111010	101?11	100
4 PERNIS	111111	012010	001111	011100	211011	111?10	100
5 MACHAERH	210031	111010	102010	110101	201011	101?1?	10?
6 ELANUS	001011	202111	112101	101110	101000	111211	100
7 ICTINIA	101011	012?11	001111	301101	110011	101?11	101
8 MILVUS	011110	201?11	100101	?01111	111011	101?10	101
9 HALIASTU	110111	202011	110001	110011	211111	111?10	101
10 HALIAEET	110011	001011	001010	111112	201011	101?11	101
11 ICHTHYOP	??????	??????	??????	??????	??????	??1?11	101
12 GYPOHIER	100111	212011	101100	311000	200001	001?11	100
13 NEOPHRON	100001	102211	010111	111020	201011	101?10	100
14 GYPAETUS	110021	111211	110000	111100	201011	100?01	101
15 NECROSYR	100111	212001	111011	100110	001011	001101	101
16 GYPS	100111	101301	110011	110100	001021	101?00	100
17 AEGYPIUS	110111	210101	000000	001100	201021	101?10	101
18 CIRCAETU	210021	2?1011	110100	011100	201011	111?11	101
19 TERATHOP	200021	001011	112100	111002	201011	001211	101
20 SPILORNI	101021	102111	110101	111102	211011	111?11	101
21 POLYBORO	100121	002211	010100	110100	010010	001?11	101
22 CIRCUS	100011	201111	012111	111111	211011	011?11	101
23 MELIERAX	111111	201311	102110	311101	010011	111?11	101
24 ERYTHROT	110101	111011	111100	111011	111000	111?10	101
25 ACCIPITE	111121	201111	002001	311111	010000	111211	101
26 KAUPIFAL	211111	1?????	??????	??????	??????	??1?11	101
27 LEUCOPTE	110021	201111	111010	311111	111011	101?11	101
28 BUTEOGAL	110011	1?????	??????	??????	??????	??1?11	101
29 HETEROSP	210011	1?????	??????	??????	??????	??1?11	101
30 BUSARELL	010121	2?????	??????	??????	??????	??1?11	101
31 GERANOAE	010001	111111	100000	101101	111011	101?11	101
32 BUTEO	110121	111111	110000	110111	101011	111311	101
33 PARABUTE	110121	1?????	??????	??????	??????	??1?11	101
34 MORPHNUS	010111	102111	102011	111110	010011	111?11	101
35 HARPIA	110021	101011	100110	311102	001011	111?11	101
36 PITHECOP	200121	002011	100100	110100	010011	111?11	101
37 AQUILA	110001	100101	111110	2??012	211021	101311	101
38 HIERAAET	000021	2?????	??????	??????	??????	??1?11	101
39 LOPHAETU	200021	1?????	??????	??????	??????	??1?11	101
40 SPIZAETU	110111	1?????	??????	??????	??????	??1?11	101
41 STEPHANO	100101	102011	100100	111100	011011	111311	101
42 POLEMAET	201011	201011	111101	311112	201000	111?11	101
43 GERANOSP	110121	201011	000001	111110	11100?	11???1	101
44 HARPAGUS	111131	112111	010111	311111	011011	10????	100
45 HARPAGOR	111011	101010	100101	111101	101011	101311	101

Appendix 5.2 (continued)

Node	P PPPPPPE EEEEE1 567890	PPP EEEFFF 111EEE 123123	FFFFFF EEEEEE 456789	FF FFFFEE EEEE11 111133 0123AB	FFFFFF EEEEEE 111111 456789	FFFFFF EEEEEE 222222 012345	FFF EEE 222 678
1 SAGITTAR	110111	031101	001110	034101	222112	214102	001
2 PANDION	002120	131010	012004	022140	112100	124202	010
3 ELANOIDE	111201	111001	311000	002121	032010	103102	011
4 PERNIS	111301	121001	413002	112101	022110	003112	011
5 MACHAERH	?1???1	1??011	310002	002041	222101	102004	614
6 ELANUS	111101	110001	313003	102121	122110	112111	211
7 ICTINIA	111001	110001	310001	112001	002100	102000	511
8 MILVUS	111001	111011	313001	100001	222100	112002	011
9 HALIASTU	111101	111001	313002	100001	220123	112100	211
10 HALIAEET	111001	111001	213002	002001	120135	110104	610
11 ICHTHYOP	111001	111011	313000	112200	102000	021202	211
12 GYPOHIER	111101	111011	310001	002201	020110	124002	210
13 NEOPHRON	111301	141001	312000	113201	122112	114002	601
14 GYPAETUS	111101	111001	313000	012201	122110	102202	211
15 NECROSYR	112101	111001	313001	101211	032110	110202	610
16 GYPS	111111	111011	313000	012000	222104	212003	210
17 AEGYPIUS	112101	111001	313000	012201	230102	112002	400
18 CIRCAETU	111301	110001	310001	100221	022110	104105	610
19 TERATHOP	111101	141001	310000	000001	122110	115002	210
20 SPILORNI	111001	110001	313000	100201	022104	200102	214
21 POLYBORO	112101	120011	310000	102201	201112	112000	211
22 CIRCUS	111001	110011	313002	000201	122102	111102	612
23 MELIERAX	111301	110011	113001	111321	200110	112100	414
24 ERYTHROT	111001	110???	???00?	??????	??????	??????	???
25 ACCIPITE	111001	100011	113001	100001	102110	111103	411
26 KAUPIFAL	112001	110011	113001	010021	200112	110112	211
27 LEUCOPTE	111001	110011	113002	101021	122110	114104	014
28 BUTEOGAL	111301	101011	310001	102201	220110	112102	611
29 HETEROSP	111201	100011	113001	102021	222102	112102	114
30 BUSARELL	111001	100011	313002	102201	022102	013202	414
31 GERANOAE	111001	110011	113002	002021	120100	114102	614
32 BUTEO	111001	100011	114002	000221	100110	111100	414
33 PARABUTE	112301	120011	114000	102021	120114	011112	414
34 MORPHNUS	111001	110011	113001	112121	202100	110206	610
35 HARPIA	111301	101011	313000	001201	220100	110104	210
36 PITHECOP	111001	111011	314000	010011	002100	100102	410
37 AQUILA	111001	100011	110001	001221	222102	012104	210
38 HIERAAET	111001	100011	110001	000001	002100	112202	210
39 LOPHAETU	111301	100011	313000	102021	222120	110212	314
40 SPIZAETU	111301	100011	113001	000001	220100	112112	213
41 STEPHANO	111201	100001	314001	102311	022120	011202	610
42 POLEMAET	111001	101011	313002	011331	122102	114104	214
43 GERANOSP	111301	100011	113002	002021	100112	011112	014
44 HARPAGUS	111201	110001	313000	100021	222100	112110	211
45 HARPAGOR	111?01	100001	310002	012021	112102	114104	511

Appendix 5.2 (continued)

Node	FFFFFF EEEEEE 233333 901234	FFFFFF EEEEEE 333334 567890	FFF EEETTT 444III 123123	TTTTTT IIIIII IIIIII 456789	TTTTTT IIIIII 111111 012345	TTTTTT IIIIII 111122 678901	TTT III 222 234
1 SAGITTAR	120001	111000	100010	110110	412100	400111	120
2 PANDION	010001	102500	100001	000000	700100	201110	100
3 ELANOIDE	022001	102020	000111	010110	610000	410001	000
4 PERNIS	121111	102420	001110	010110	402100	410011	010
5 MACHAERH	022011	102111	000111	002100	210000	400010	100
6 ELANUS	022001	100000	000111	410100	001000	200001	101
7 ICTINIA	001111	112120	000111	002110	210004	001000	000
8 MILVUS	021101	102100	000111	000100	200100	400000	100
9 HALIASTU	021011	102101	010111	402100	200100	400000	000
10 HALIAEET	001001	002301	101111	411100	100103	101000	002
11 ICHTHYOP	101001	102101	001111	411120	200103	100010	002
12 GYPOHIER	121101	010220	000111	000100	400001	402000	100
13 NEOPHRON	111111	002121	001111	111100	402101	400011	110
14 GYPAETUS	101011	002101	001111	000110	600101	400010	100
15 NECROSYR	121111	012121	101111	000110	400000	201001	100
16 GYPS	131011	002121	100111	400110	402100	221001	101
17 AEGYPIUS	111211	012100	001111	001110	401?00	20?001	110
18 CIRCAETU	032111	102021	000111	402111	700100	410000	101
19 TERATHOP	011001	002001	000111	012101	010000	201010	000
20 SPILORNI	101001	002101	001111	012100	500000	400001	100
21 POLYBORO	002000	102000	100111	010100	702002	402110	200
22 CIRCUS	001000	102100	110111	110101	410110	410010	002
23 MELIERAX	001000	102011	000111	102100	210004	410000	100
24 ERYTHROT	??????	??????	??????	??????	??????	??????	???
25 ACCIPITE	001001	104000	000111	112140	201004	410000	110
26 KAUPIFAL	021000	112000	000111	402100	001103	410000	000
27 LEUCOPTE	001001	104000	001111	402100	710103	21?010	000
28 BUTEOGAL	001001	112000	011111	102100	200000	402000	100
29 HETEROSP	101011	102101	001111	212101	000100	311001	100
30 BUSARELL	011010	102000	010111	202100	010000	210000	000
31 GERANOAE	001011	102000	011111	102100	000000	401000	010
32 BUTEO	011001	104001	001111	402100	510100	411001	000
33 PARABUTE	001000	012001	001111	410100	210000	410000	000
34 MORPHNUS	101011	112101	100???	??????	??????	??????	???
35 HARPIA	031011	102101	101111	301120	001100	511000	200
36 PITHECOP	101001	103121	001111	402100	011100	411000	201
37 AQUILA	001111	002101	001111	112101	001003	411000	002
38 HIERAAET	001001	104001	001111	412100	011003	401000	000
39 LOPHAETU	001011	102101	001111	402100	301104	201010	000
40 SPIZAETU	021001	102100	001111	112100	011004	411010	000
41 STEPHANO	111011	102001	001111	112101	001100	201010	000
42 POLEMAET	001001	102400	001111	102100	011003	211010	000
43 GERANOSP	021000	101101	110111	410100	202112	401111	110
44 HARPAGUS	031001	114000	001111	112130	210000	411000	100
45 HARPAGOR	001011	112100	000111	012141	001000	411000	200

Appendix 5.2 (continued)

Node	TTTTTT IIIIII 222223 567890	TTTTTT IIIIII 333333 123456	TTTTTT IIIIII 333444 789012	TT IITTTT 44MMMM 342456	CCCCC TRRRRR M11111 904125	CCC RRRCS 122RT 61556
1 SAGITTAR	102132	050102	110110	00????	?10???	????0
2 PANDION	022020	230202	000000	022?21	000???	????1
3 ELANOIDE	022002	031002	100012	022???	2102?0	00102
4 PERNIS	110030	220200	210012	002?2?	010??0	0000?
5 MACHAERH	002002	420102	200000	220???	?10230	01103
6 ELANUS	402002	040302	101112	0402?0	?10231	01104
7 ICTINIA	002131	230102	100002	200???	010320	01103
8 MILVUS	000102	471000	110011	030???	?10220	01002
9 HALIASTU	002002	421000	110012	030???	?10220	0200?
10 HALIAEET	002021	470200	110012	2200??	?10210	0200?
11 ICHTHYOP	002022	271040	110012	0300??	?10310	01?0?
12 GYPOHIER	020000	270120	100010	020?11	?10?20	0011?
13 NEOPHRON	120002	410100	110011	2201??	?10320	10132
14 GYPAETUS	122032	420110	100010	220???	?1???0	1113?
15 NECROSYR	102001	461100	000002	240???	?11200	12131
16 GYPS	000101	250000	110010	200?0?	011200	1213?
17 AEGYPIUS	100?02	4??000	20001?	24020?	011200	1213?
18 CIRCAETU	000001	470100	111014	02011?	?10220	11003
19 TERATHOP	002101	420000	210012	220?0?	?11220	1100?
20 SPILORNI	020002	430120	211011	240?11	010220	0101?
21 POLYBORO	500002	120100	200010	240??1	?10220	00031
22 CIRCUS	002000	420101	110010	040???	?10220	0110?
23 MELIERAX	002020	021101	111002	010???	?10??0	00114
24 ERYTHROT	??????	??????	??????	??0???	?10???	????3
25 ACCIPITE	101122	420000	100012	010?1?	210221	?110?
26 KAUPIFAL	002021	231202	011102	240???	?10??0	00114
27 LEUCOPTE	122002	231132	111012	200???	?10220	00114
28 BUTEOGAL	002002	471132	110012	040???	?10210	0000?
29 HETEROSP	000032	470100	100010	020???	210??0	?1003
30 BUSARELL	002002	430002	100015	040???	?10210	01003
31 GERANOAE	102001	470200	001012	040???	?10212	01003
32 BUTEO	002001	430202	011012	04031?	210210	00003
33 PARABUTE	102002	430142	011013	020???	?10220	0100?
34 MORPHNUS	??????	??????	??????	??0???	?10??0	0?0??
35 HARPIA	202001	360230	000010	000???	010310	01003
36 PITHECOP	002012	420201	011012	000???	?10220	01012
37 AQUILA	002002	420101	211014	230???	110110	0100?
38 HIERAAET	102012	430202	100100	140???	010110	0100?
39 LOPHAETU	002012	420202	011102	130???	?10??1	0100?
40 SPIZAETU	002002	370032	100012	030???	?10210	00002
41 STEPHANO	002001	320232	000112	040???	?10310	11003
42 POLEMAET	002002	430202	100012	240???	010210	1100?
43 GERANOSP	120000	430200	000011	020???	310??0	?110?
44 HARPAGUS	022012	220202	111012	24????	?10020	00104
45 HARPAGOR	000001	450300	210004	020340	200210	0201?

Appendix 5.3 Character states known for taxa not included in phylogenetic analysis.

								H	H
		CC		MMM	C	HHH		HU	UHH
		CCCRRM	MMMMMM	MMAAAP	PPOFFH	HUUUHH	HHHHU1		1UU
		RRR11A	AAAAAA	AA111H	XX2UUU	U222UU	UUUU11		312
		234781	234567	890121	120131	2ADE34	56790A		A41
1	AVICEDA	200001	010311	120100	11010?	??????	??????	???	
2	LEPTODON	000001	??????	????00	01010?	??????	??????	???	
3	CHELICTI	?0000?	??????	?????0	??011?	012111	120111	100	
4	BUTASTUR	?0000?	??????	?????0	??0111	012121	110111	010	
5	ICTINAET	?0000?	??????	?????0	??0111	200011	212113	001	
6	CHONDROH	?00001	112321	120010	110111	??????	??????	???	
7	ROSTRHAM	?00001	300111	021000	110111	??????	??????	???	
8	GAMPSONY	?00001	111120	220100	??0111	??????	??????	???	
9	ASTURINA	??????	??????	??????	??0111	??????	??????	???	
10	HARPYHAL	?0000?	??????	??????	??0111	??????	??????	???	
11	LOPHOICT	?0000?	??????	?????0	??0111	??????	??????	???	
12	OROAETUS	?0000?	??????	??????	??0111	??????	??????	???	
13	SPIZASTU	?00001	111121	11000?	??0111	??????	??????	???	
14	UROTRIOR	?00001	111121	110100	??0111	??????	??????	???	
15	HARPAGOR	2?0001	112311	121100	??0101	212121	121114	100	

		HHHHHH	H U	UUU	CC	C CCCC	CC	
		UUUUUU	UUULUU	UULLLC	CCCCMM	MCMMMM	MMSSSP	PPP
		222223	3LL3LL	LL111M	MMMM77	7M1111	11TTTE	EEE
Node		456791	212A45	791231	3467AB	C80123	461231	234
1	AVICEDA	??????	??????	??????	??????	??????	??1?10	100
2	LEPTODON	??????	??????	??????	??????	??????	??1?1?	10?
3	CHELICTI	21?011	20?110	10110?	??1??1	0?10??	??1?10	10?
4	BUTASTUR	210011	201110	100100	211111	20?010	1?1?11	101
5	ICTINAET	201011	?02211	110010	111112	211011	101?11	101
6	CHONDROH	??????	??????	??????	??????	??????	??????	10?
7	ROSTRHAM	??????	??????	??????	??????	??????	??????	10?
8	GAMPSONY	??????	??????	??????	??????	??????	??????	10?
9	ASTURINA	??????	??????	??????	??????	??????	??????	10?
10	HARPYHAL	??????	??????	??????	??????	??????	??????	10?
11	LOPHOICT	??????	??????	??????	??????	??????	??????	10?
12	OROAETUS	??????	??????	??????	??????	??????	??????	10?
13	SPIZASTU	??????	??????	??????	??????	??????	??????	10?
14	UROTRIOR	??????	??????	??????	??????	??????	??????	10?
15	HARPAGOR	111011	101010	100101	111101	101011	101311	101

Appendix 5.3 (continued)

Node	PPPP PPPPPE EEEEE1 567890	EEEFFF 111EEE 123123	FFFFFF EEEEEE 456789	FF FFFFEE EEEE11 111133 0123AB	FFFFFF EEEEEE 111111 456789	FFFFFF EEEEEE 222222 012345	FFF EEE 222 678
1 AVICEDA	111101	111011	313000	012141	222102	103102	011
2 LEPTODON	?1???1	1?????	???00?	??????	??????	??????	???
3 CHELICTI	?1???1	1????1	?1?00?	??????	??????	??????	???
4 BUTASTUR	111001	100???	???00?	??????	??????	??????	???
5 ICTINAET	111301	100???	???00?	??????	??????	??????	???
6 CHONDROH	11???1	1??001	310000	002221	022000	103110	011
7 ROSTRHAM	11???1	1??001	310001	101201	220102	012102	611
8 GAMPSONY	11???1	1??001	513001	104201	000114	102112	411
9 ASTURINA	11???1	1?????	???00?	??????	??????	??????	???
10 HARPYHAL	11???1	1?????	???00?	??????	??????	??????	???
11 LOPHOICT	11???1	1?????	???00?	??????	??????	??????	???
12 OROAETUS	11???1	1?????	???00?	??????	??????	??????	???
13 SPIZASTU	11???1	1??011	314001	110021	122114	112102	711
14 UROTRIOR	11???1	1??001	213000	002221	122100	110112	414
15 HARPAGOR	111?01	100001	310002	012021	112102	114104	511

Node	FFFFFF EEEEEE 233333 901234	FFFFFF EEEEEE 333334 567890	FFF EEETTT 444III 123123	TTTTTT IIIIII 456789	TTTTTT IIIIII 111111 012345	TTTTTT IIIIII 111122 678901	TTT III 222 234
1 AVICEDA	022101	102010	000110	412110	202102	410011	200
2 LEPTODON	??????	??????	??????	??????	??????	??????	???
3 CHELICTI	??????	??????	???111	1?????	?01004	21101?	000
4 BUTASTUR	??????	??????	??????	??????	??????	??????	???
5 ICTINAET	??????	??????	??????	??????	??????	??????	???
6 CHONDROH	022100	102420	000111	010100	201000	412000	110
7 ROSTRHAM	001010	102000	001111	412140	210000	401001	010
8 GAMPSONY	020001	102000	000111	102110	201000	212000	000
9 ASTURINA	??????	??????	??????	??????	??????	??????	???
10 HARPYHAL	??????	??????	???111	402140	700000	201000	200
11 LOPHOICT	??????	??????	??????	??????	??????	??????	???
12 OROAETUS	??????	??????	??????	??????	??????	??????	???
13 SPIZASTU	001011	102601	001101	112110	701100	202010	000
14 UROTRIOR	001001	102601	001111	112100	710000	411000	010
15 HARPAGOR	001011	112100	000111	012141	001000	411000	200

Appendix 5.3 (continued)

Node	TTTTTT IIIIII 222223 567890	TTTTTT IIIIII 333333 123456	TTTTTT IIIIII 333444 789012	TT IITTTT 44MMMM 342456	CCCCC TRRRRR M11111 904125	CCC RRRCS 122RT 61556
1 AVICEDA	020002	070022	200010	031???	?10320	0010?
2 LEPTODON	??????	??????	??????	??03?1	010???	????3
3 CHELICTI	122101	071002	2010?0	000???	?10???	?????
4 BUTASTUR	??????	??????	??????	??0???	?10220	0000?
5 ICTINAET	??????	??????	??????	??0???	?10???	?????
6 CHONDROH	100001	001020	100010	03???1	010320	?1?0?
7 ROSTRHAM	000102	430200	110012	02????	?10220	?1?0?
8 GAMPSONY	302000	240002	110111	00???0	?10321	0010?
9 ASTURINA	??????	??????	??????	??????	?10???	?????
10 HARPYHAL	002032	400022	101000	22????	?10???	?????
11 LOPHOICT	??????	??????	??????	??????	?10???	?????
12 OROAETUS	??????	??????	??????	??????	?10???	?????
13 SPIZASTU	102031	420202	111010	23????	?10210	0000?
14 UROTRIOR	102001	430202	110012	02????	?10320	00014
15 HARPAGOR	000001	450300	210004	020340	200210	0201?

Appendix 5.4 Number of species in each genus of Accipitridae in each of 18 geographical areas (Fig. 5.16).

Node		P AALCPH NVEHEE DIPORN ICTNNI	E GLMLRI AAAAON MNCNSI POHUTA	E T R O AA PHPMLL AAHIII GMOLAA UIIVSA	I CGNEYG HYECPY TPORAP HOPOES	C NG ERTSDE GCEPRU YARIYT PEALOR	C AI EPRERM ROCLOE ALUITG NYSERA	G IMU E RK YAA TCU HCP
1	NORTHAM	100000	010111	000001	000000	000000	001000	030
2	CENTRAM	001100	110111	100000	000000	000000	100000	040
3	WINDIES	100100	000010	000000	000000	000000	000000	020
4	SOUTHAM	001100	110121	200000	000000	000000	102000	050
5	SOUTHAF	110000	001100	000101	011113	241010	012310	081
6	NORTHAF	100000	000100	000200	001012	110000	002100	010
7	MADAGAS	000000	001100	000101	000000	000001	012000	010
8	EUROPE	100010	000100	000201	001011	110000	004000	030
9	MIDEAST	100000	000100	000201	001011	210000	004100	040
10	NORTHAS	100010	000000	000103	000012	110000	005000	050
11	SEASIA	120010	000100	000112	201003	110300	000000	040
12	INDOPHI	110020	001100	000111	200002	100300	000000	060
13	NEWGUIN	110001	001100	000121	000000	000000	001001	090
14	MELANES	110001	000000	000122	000000	000000	001000	0A0
15	AUSTRAL	110000	000200	011121	000000	000000	002000	130
16	NEWZEAL	000000	000000	000001	000000	000000	001000	010
17	OCEANIA	000000	000000	000001	000000	000000	001000	000
18	GREENLA	000000	000000	000001	000000	000000	000000	000

Node		B H BLUHAB UETERU TUETPS ACOEYA SOGRHR	G EBMAC PRUORT AATRPI RNEPIN AOOHAA	HI H HASS APIQPP RIEUII PTRIZZ YHALAA OEAASE	L OOPS H PROT A HOLESR AAEPAP EEMHGA	C H E L I C
1	NORTHAM	001000	107000	000100	000000	0
2	CENTRAM	023111	106110	000112	000000	0
3	WINDIES	000000	004000	000000	000000	0
4	SOUTHAM	083121	118110	000012	010000	0
5	SOUTHAF	100000	003000	002301	101110	0
6	NORTHAF	000000	001000	001300	000000	1
7	MADAGAS	000000	001000	000000	000000	0
8	EUROPE	000000	003000	002500	000000	0
9	MIDEAST	000000	002000	002300	000000	0
10	NORTHAS	100000	004000	002401	000000	0
11	SEASIA	200000	000001	002202	000000	0
12	INDOPHI	200000	000001	012003	000000	0
13	NEWGUIN	000000	000001	101100	000000	0
14	MELANES	000000	000000	000000	000000	0
15	AUSTRAL	000000	000000	001100	000000	0
16	NEWZEAL	000000	000000	000000	000001	0
17	OCEANIA	000000	002000	000000	000000	0
18	GREENLA	000000	000000	000000	000000	0

CHAPTER 2

6. CHAPTER 2
REDESCRIPTION OF *HARPAGORNIS MOOREI* HAAST, 1872

6.1 INTRODUCTION

Apart from the original descriptions of the limited material available to early researchers (Haast 1872, 1874, 1881; Hamilton 1893, 1894; Owen 1879), little has been published on the skeletal anatomy of *Harpagornis moorei* Haast, 1872. Oliver (1930, 1955) gave abbreviated diagnoses of both nominal taxa described by Haast, *Harpagornis moorei*, and *H. assimilis* Haast, 1874. He also discussed the structure of the palate as it was then known (Oliver 1945). Scarlett (1972) provided illustrations and measurements of larger bones likely to be found in archaeological sites. A photograph of a mounted composite skeleton from Castle Rocks, southwest of Lumsden in western Southland, has been reprinted several times (e.g., Lambrecht 1933; Oliver 1930, 1955).

Most writers (e.g. Duff 1949, Lambrecht 1933, McCulloch 1982, Rothschild 1907) have reprinted or reinterpreted previously published descriptions. Errors of fact and interpretation have crept in and accumulated in both scientific and popular literature.

The first problem, that of the taxonomic status of the second named species, *Harpagornis assimilis* Haast, 1874, is dealt with in Section 6.4 and Chapter 2A (Section 7). Briefly, I concluded that the name *Harpagornis assimilis* Haast, 1874 is a junior subjective synonym of *Harpagornis moorei* Haast, 1872 and that the name was given to an individual of the smaller sex of a sexually size-dimorphic species. These conclusions confirmed the predictions of the original author. Hereafter, I will refer all material to the senior named taxon.

It then had to be established that all the material referred to *Harpagornis moorei* had been correctly determined. As material referred to the taxon included specimens up to 35,000 and possibly 80,000 years old, and specimens of rare elements had been determined by size as much as any discerned morphological character, the possibility existed that material from other accipitrids or even other higher taxa had been included. There was also the possibility of anagenetic change over such a time span, as has been demonstrated

in dwarfing lineages of macropodid marsupials by Marshall & Corrucini (1978) and in moas (Worthy 1987).

Most parts of the skeleton of *H. moorei* are now represented in collections, and sample sizes of many elements are adequate for basic statistical analysis. Some specimens are perfectly preserved, and compare favourably with freshly prepared material; most major elements are represented by at least one such specimen. In addition, there are now two tolerably complete associated skeletons which allow interside and intermembral comparisons of dimensions. I have taken advantage of the abundance of new material, and of the existence of irrefutably associated material, to redescribe the genus and species.

A brief redescription of *Harpagornis moorei* is desirable because previous descriptions covered only a limited range of elements. Material from some sites has been referred to the taxon largely on the basis of size, and it is now clear that several bones catalogued in various institutions as *Harpagornis moorei* do not belong to that taxon. A redescription based on the copious, positively referred material now available will facilitate identification of new material, and make the material more accessible for comparative studies of accipitrid anatomy.

Existing descriptions and illustrations are also scattered through old and somewhat obscure publications. Therefore, in addition to the redescription, I have taken the opportunity to reproduce some of the more important early figures here, and to provide photographs of most elements of the skeleton.

Anatomical terms are from Baumel et al. (1979) and Ballmann (1969, 1973). The original description is included before my description of each element. Other descriptions and illustrations of separate elements from Haast (1874, 1881), Owen (1879), and Hamilton (1894) are also repeated, for completeness.

My descriptions are based on characters noted in several papers on accipitrids (Ballmann 1969, 1973; Jollie 1976, 1977a, 1977b, 1977c; Olson 1982, 1987), and my own studies of the osteology of the Accipitridae. In general, characters used in my cladistic study of the Accipitridae are not repeated here (see Chapter 1).

6.2 MORPHOLOGICAL TERMS, AND DIMENSIONS

The morphological terms used in descriptions of each element follow Howard (1929), Ballmann (1969, 1973) and Baumel (1979). The dimensions and primary landmarks (or homologous points; H-points in Levinton (1988)) for measurements are shown in Fig. 4.1 in the General Methods section. The dimension system was adopted as one applicable to a wide range of accipitrid taxa. Some dimensions require that the element is set, or held against, a plane surface, but most can be taken with Vernier callipers across clearly defined landmarks.

Dimensions were biased towards lengths, widths, and shaft diameters. A truss system (in which landmarks (homologous points) are chosen in a grid system across the whole plane) as advocated by Strauss & Bookstein (1982) would have been preferable, because the statistics derived are relatively unbiased, and potentially yield much more information on shape and differences in shape. This approach was not adopted because the differences between this and other taxa are clearly defined on non-mensural characters, and the additional discrimination possible did not warrant the increased complexity both of measurement and of analysis.

6.3 REDESCRIPTION OF *HARPAGORNIS MOOREI* HAAST, 1872 (AVES: ACCIPITRIDAE)

6.3.1 Review of previous descriptions - an annotated bibliography of descriptive work on *Harpagornis moorei*

1872 Haast *Original description* Haast described *Harpagornis Moorei* from "a femur, a few ungual phalanges, and one rib, all belonging doubtless to the same individual," (Haast 1872: 192). His descriptions were illustrated by Dr Llewellyn Powell (Plate X, fig. 1, 4, 5; Plate XI, fig. 1, 1a, 2, 5, in Haast 1872). Relevant sections of the original description are included below, in appropriate places.

1874 Haast described further material from near the original site at Glenmark, and referred it to his *Harpagornis moorei.* Material, including several of the principal bones of a single skeleton, from a second site nearby, were described as the types of a new species, *Harpagornis assimilis.*

1879 Owen redescribed the main bones known at the time from casts and photographs sent to him by Haast. He included a description of a complete pelvis.

1880 Haast described the mandible and other elements found at a newly discovered site, Hamilton Swamp in Central Otago.

1893 Hamilton listed all the material known to him, and described and illustrated the skull from a specimen that he had just recovered from a fissure at Castle Rocks, in western Southland.

1894 Hamilton described further elements, including a complete sternum, from a new collection of material of the first skeleton, and from a nearly complete second skeleton found with the first.

1896 Shufeldt examined photographs of specimens from Castle Rock and compared them with specimens of several species of large eagle.

1907 Rothschild repeated Haast's and Owen's descriptions, stressing the size of the bird, and the relative shortness of the ulna.

1930 Oliver recognised and gave diagnoses for the genus and both species.

1933 Lambrecht summarised Haast's, Owen's, and Oliver's descriptions, and gave a summary of the geographical distribution.

1945 Oliver described the basic structure of the palate, as it was then known, and compared it with *Aquila* and *Haliaeetus*, favouring a relationship with the latter. He also briefly noted features of the sternum and pelvis.

1955 Oliver repeated his 1930 diagnoses with slight differences in wording, and included new sites recorded since 1930.

1972 Scarlett illustrated 11 elements, and gave ranges for length for femur, tibiotarsus, tarsometatarsus, humerus, ulna, and radius.

6.5.3 STATUS OF *HARPAGORNIS ASSIMILIS* HAAST, 1874

The first problem I had to resolve was whether *Harpagornis assimilis* Haast, 1874 is a valid taxon. As Haast diagnosed this taxon by its smaller size, it is appropriate to examine its validity on mensural grounds. If *H. assimilis* was a separate species, the size-independent variation in element lengths for the combined sample (*H. moorei* plus *H. assimilis*) would be greater than that found within the living species (in this instance, *Harpia harpyja*), but of the same order as between-species variation in a group of living species.

This was tested by comparing basic statistics of the dimensions of the major skeletal elements with those of a very large living species of accipitrid. The Methods and Results of this investigation are presented and discussed in Chapter 2A, Section 7 of this thesis, a paper published in *New Zealand Natural Sciences*.

Material referred to *Harpagornis moorei* and *H. assimilis* was also compared directly with type material, and key referred material. These comparisons supported the conclusion based on measurements of the major axial and limb bones, namely that there was only one taxon represented in the material.

The process of assessing whether an isolated specimen should be referred to *Harpagornis moorei* was based on the following protocol: a comparison of type material of the two nominal species to confirm their identity, to increase the range of positively referred elements (because more of the skeleton was

available for *H. assimilis* than for *H. moorei*), with most emphasis being placed on morphology of the femur, which is the most information-rich element represented in both type series; a comparison of the *H. moorei* femora with those of other taxa which may have been present in New Zealand at some time, including *Aquila audax*, and *Haliaeetus leucogaster* (thereby also eliminating the endemic *Haliaeetus australis*, of which the femur is presently unknown (P R Millener pers. comm., 17 Jan 1991) to eliminate the possibility of confusion with possible vagrant species or former (now extinct) residents; comparison of the femora and expanded type series which homologous bones from individuals with better element representation, in particular the substantially complete skeletons catalogued as OMNZ C40.8, and NMNZ S27773, to confirm that only one endemic taxon was involved; where an element was represented in the series, cross-checking back to elements from the type locality.

It is extremely unlikely that any specimens already referred to *Harpagornis moorei* came from another species of accipitrid. Haast discriminated between his taxa on size and the major axial and appendicular bones of large accipitrids found so far on the two main islands of New Zealand have been shown elsewhere (Holdaway 1990a) to have size distributions consistent with their belonging to only one species. The species had a temporal range from at least the penultimate (Oturian) interglacial, to the late Holocene (see Chapter 3 - Section 8).

Haast (1874) referred material from the type site to *H. moorei*, and stated that he could not distinguish between elements in the two type series on the basis of their morphology. It should be noted that he regarded the referred material of *H. moorei* as part of the type series, but it has no standing as such under the present *International Code of Nomenclature* (ICZN 1985). Until the discovery of the Mount Owen specimen (NMNZ, S 27773), the most complete associated skeleton was the smaller individual from Castle Rocks, Southland, excavated by Hamilton and others in 1893 (OM C 40.8), and the association of minor elements with the name-bearing types was problematical.

Both type series from Glenmark were fragmentary, and lacked crania, sterna, and most elements of the axial skeleton and digits of both wing and feet.

Although the fissure deposit at Castle Rocks contained the remains of at least two birds (OM C 40.8; NMNZ DM2134), several bones, such as the os ulnare and os radiale, os pterygoideus, and hyoid apparatus were missing, and the sets of vertebrae and pedal phalanges were incomplete.

It is also usually impossible to be sure that material found together came from the same individual. Even where left and right side elements from a single site agree within a millimetre in length, the association is usually not unequivocal. This is demonstrated by the collections from Enfield Swamp, where it is impossible to say on bone length which of two right ulnae belongs with the single left ulna. The problem of allocation of bones among individuals was partly solved by the recovery of the Mount Owen specimen. In the more than 90 separate bones collected at that site, there are no duplicates, and the characteristics and small size of the site make it certain than only one animal was present. Fortunately, too, the bones were generally in excellent condition. The only elements missing from the Mt Owen specimen were most of the scleral ossicles, a caudal element from one side of the hyoid apparatus, the second phalanx of the major digit of the left wing (the right one is present), and the accessory bone at the carpal flexure usually present in accipitrids (Bock & McEvey 1964). It is possibly the most complete fossil or subfossil skeleton of an extinct bird of prey.

As a basis for further comparisons, I compared the lectotype femur (Holdaway 1990a) from Glenmark with the lectotype femur from the type series of H. assimilis, and with the femora of the two associated skeletons noted above. All the femora agreed in detail with the lectotype femur from Glenmark (see below).

Once the identity of the three series had been confirmed on the basis of the morphology of the femur, as well as on mensural grounds, the Mt Owen specimen was used as the standard for comparisons. Elements were rejected if they did not match the morphology of the corresponding element in the two type series, or in the key individuals noted above, and if they possessed features characteristic of groups other than the accipitrids.

Most identifications of isolated elements from other sites were confirmed. The few misidentifications have proved to be elements of taxa from other families, and do not represent other large accipitrids. For most elements, sample sizes were large enough for levels of individual variation in characters to be assessed.

6.5 SYSTEMATIC PALAEONTOLOGY

Order CICONIIFORMES (sensu Sibley et al. 1988)
Family ACCIPITRIDAE Vieillot, 1816

Diagnosis. (Pycraft 1902: 318-319; Friedmann 1950: 64-65): coracoids not overlapping at sternum; no bony ring on proximo-cranial surface of tarsometatarsus; 4th toe not reversible; claws graduated in size from 1st (largest) to 4th (smallest); claws flat or rounded on ventral surface; palate indirectly desmognathous, rarely schizognathous; vomer not expanded anteriorly, not closely applied to palatines [unknown in *Harpagornis moorei*]; prefrontals (*sensu* Baumel 1979, termed lachrymals in Friedmann 1950) with accessory superciliary plate; "antorbital plate" (ectethmoid) reduced, often tongue-shaped, articulating or even fused by its free end with distal extremity of lachrymal; squamosal prominence (process) not strongly developed; ventral surface of maxilla without median bony ridge; mandibular ramus without ramal vacuity; nasal canal incompletely ossified, with large, pyriform external opening, exposing nasal septum; no central bony tubercle to naral opening (sometimes with a cartilaginous) central tubercle, or, if slitlike, a tubercle at lower posterior angle, or if opening small and more or less circular without bony rim or tubercle; procoracoid small, articulating with scapula only and widely separated from clavicle; thoracic vertebrae all free; spina interna sterni absent; postacetabular ilium shorter than ischium, much deflected; ischium never produced backwards as spine; pubis often vestigial.

Separated from vulturid vultures (still included as falconiforms by many taxonomists) by the hallux's being incumbent and functional and much more than half as long as fourth toe, by the tarsometatarsus being greatly flattened, with strong lateral ridges (the inner one produced and thin), and its proximo-plantar surface having two ridges separated by a deep and wide groove. The basipterygoid processes are rudimentary. The ilio-ischiadic margin of the pelvis is unnotched. The external nares are imperforate, and the olfactory chamber is small, and the maxillo-palatines are spongy.

Subfamily Accipitrinae Vieillot, 1816

Genus *Harpagornis* Haast, 1872

Type species. *Harpagornis moorei* Haast, 1872 (by monotypy).

Diagnosis. Large accipitrids, with the characters of the family (Pycraft 1902; Friedmann 1950). Distinguished by the narrow and dorso-ventrally compressed skull, the presence of a well-developed scroll of bone around the nostril in the external nares, posterior cranium sharply angular in lateral view, broad maxillary process, a relatively short ulna, pelvis with very sharp ilio-ischiadic angle and expanded iliac fossae.

6.5.3 Status of genus *Harpagornis* Haast, 1872

In Chapter 1, I showed that *Harpagornis moorei* is the sister group of *Aquila.* It would, however, be premature to submerge *Harpagornis* in *Aquila*, at the present state of knowledge of the generic systematics of *Aquila* (Amadon 1982a), so I retain Haast's genus here.

Harpagornis moorei Haast, 1872

(Plates 1-16)

1872 *Harpagornis Moorei* Haast, p. 193, pl. X, fig. 1, 4, 5; pl. XI, fig. 1, 1a, 2, 5).
1874 *Harpagornis moorei* Haast; Haast, p. 62, pl. VII, fig. 1-6, pl. IX, fig. 1-3, 3a
Harpagornis assimilis Haast, p. 64, pl. VIII, fig. 1-7.
1879 *Harpagornis moorei* Haast; Owen, 1 p. 141, 2, pl. CV, fig. 1-4, pl. CVI, fig. 1-6, pl. CVII, 1-7.
1881 *Harpagornis assimilis* Haast; Haast, p. 232, pl. XIII, fig. 1-4.
1891 *Harpagornis moorei* Haast; Lydekker, p. 25.
Harpagornis assimilis Haast; Lydekker, p. 25, as (queried) synonym of *H. moorei.*
1893 *Harpagornis moorei* Haast; Hamilton, p. 92, pl. VII, C, D.
Harpagornis assimilis Haast; Hamilton, p. 93, as male of *H. moorei.*

1894 *Harpagornis assimilis* Haast; Hamilton, p. 227, pl. XXIII, fig. 1-3 (as male of *H. moorei*).
Harpagornis moorei Haast; Hamilton, p. 227, pl. XXIII, fig. 4.
1898 *Harpagornis moorei* Haast; Beddard, p. 484.
1907 *Harpagornis moorei* Haast; Rothschild, p. 85.
1930 *Harpagornis moorei* Haast; Oliver, p. 392, unnumbered fig.
Harpagornis assimilis Haast; Oliver, p. 394.
1933 *Harpagornis Moorei* Haast; Lambrecht, p. 410, fig. 135, gives date as 1871.
Harpagornis assimilis Haast; Lambrecht, p. 410, as synonym of *H. moorei*, gives date as 1873.
1945 *Harpagornis moorei* Haast; Oliver, p. 137, fig. 46.
Harpagornis haasti Haast; Oliver, caption to fig. 46 (lapsus)
1955 *Harpagornis moorei* Haast; Oliver, p. 604, unnumbered fig. (specimen referred to *H. assimilis* by Hamilton (1894)
Harpagornis assimilis Haast; Oliver, p. 605.
1964 *Harpagornis moorei* Haast; Brodkorb, p. 272.
Harpagornis assimilis Haast; Brodkorb, p.273 (as synonym of *H. moorei*)
1970 *Harpagornis moorei* Haast; Kinsky et al., p. 78.
Harpagornis assimilis Haast; Kinsky et al., p. 78 (as synonym of *H. moorei*)
1972 *Harpagornis moorei* Haast; Scarlett, p. 11-12, pl. 3, 5, 7, 9, 10, 11, 20.

Diagnosis. Oliver (1930: 392): "Large extinct eagles with very strong legs but comparatively short wings. *Harpagornis* is closely related to the recent genus *Aquila.* Its distinctive features are the narrow skull, short ulna and stout tarso-metatarsus. As in *Aquila* the femur is longer than the tarso-metatarsus."

Oliver (1945: 137): "The giant eagle of New Zealand, ..., was compared by Shufeldt with *Aquila.* By the form of the skull, however, it should be placed nearer to Haliæëtus. In fact, it is further from *Aquila* than is *Haliæëtus."*

Oliver (1955: 604): "Large extinct eagles with very strong legs but comparatively short wings. *Harpagornis* is closely allied to the recent genus *Haliaetus* (sic). Its distinctive features are the narrow skull, short ulna and stout metatarsus."

Characters of family. From *Aquila* by much larger size; narrow, low cranium; nasal scroll (present in some individuals of *Aquila*); elongated external nares;

caudal margin of Proc maxillare Os nasale entire, not notched to receive rostral angle of Os prefrontale as in *Aquila* greater depth of thoracic vertebrae; ventral margin of coracoidal sulcus more caudal than in *Aquila*, not obscuring dorsal margin in ventral view; pilum sterna visible inside sternal bowl as flat-topped ridge with lateral furrows, not visible in *Aquila*; spina externa deeper than broad, broader than deep in *Aquila*; steeper pre-postacetabular angle than in *Aquila*; ilio-ischiadic foramen produced postero-dorsally (a 'rounded triangle'), oval in *Aquila*; ischial bar with distinct pit; anterior iliac plates produced dorsally above synsacrum, leaving deep dorsal fossa;

Type material. Left femur, 2 pedal ungual phalanges, 1 rib, AV 5104 pt, F R Fuller [J Haast], Mar 1871. Femur designated as **lectotype** in Holdaway (1990a).

Type locality and stratum. Holocene peat bed along stream course, 5-6 ft [1.5-1.8 m] below surface, near Glenmark Creek (Omihi Creek) [Glenmark 5], c 60 km north of Christchurch, South Island, New Zealand; 43°01'00"S, 172°47'00"E; Grid reference NZMS1 S68/69 141187, NZMS 260 N34/921992, c 80 m asl.

6.5.8 REDESCRIPTION

6.5.8.1 General Each element is described in a separate section, with separate lists of material for each. Previous descriptions are repeated here, where available, for convenience of comparison. References to published figures are also included. States of characters used in the phylogenetic analysis (Chapter 1) are not included, but are listed in the character matrix (Appendix 5.1) at the end of Chapter 1. Figures from Haast's papers and Owen (1879) are reproduced here as Fig. 6.1 (A-I), by permission of the Royal Society of New Zealand, Inc.

A complete list of localities and sites is given, with location, co-ordinates, and altitudes, in Chapter 3; abbreviated names are used here.

In the tables of measurements, all means are systematic under-estimates because of the system of minimum measurements used to maximise the sample sizes. Statistics were calculated from measurements of the left member of an

individual where possible; that is, where both were available and intact. Where a measurement of a right side member was more reliable, it was used instead. Where an individual was represented by an element from one side, that measurement was included regardless of side. Where elements from both sides of one individual were both worn, the measurement from the least worn element was used. Under-estimates resulting from slight wear is denoted by the minimum measurement (as taken) followed by a + sign. If wear was judged to be severe, and the resulting measurement was likely to be >> 1% in error, the minimum value is followed by ++. In some instances, an estimate was made of the dimension of a reconstructed element, where a whole section or sections were missing or very badly worn: this is denoted by ±. Estimates denoted by ++ or ± were not used in compiling statistical summaries.

Other conventions used in the tables are: -, indicates landmarks too worn for meaningful measurement; *, indicates approximate value, not used in computation of statistics; ?, indicates probable site, but uncertain, see text;, space in locality column indicates probable pairing of bones as contralateral sides of same individual.

6.5.8.2 *CRANIUM AND PREMAXILLA*

Hamilton (1893: pl. VII, C, D; 1894: pl. XXIII, 1)

Oliver (1930: 392): "Skull long with a deep powerful beak decurved at the tip and with the cutting edge arcuate. Cranium suddenly widening behind orbits; temporal fossae large and shallow, the ridges confluent with the lambdoidal ridges."

Oliver (1945: fig. 46, as *Harpagornis haasti*): "By the form of the skull, however, it should be placed nearer to *Haliaeetus.* In fact, it is further from *Aquila* than is *Haliaeetus*).

Oliver (1955: 604): "Skull long with a deep powerful beak decurved at the tip and with the cutting edge sinuate. Cranium abruptly widening behind orbits; temporal fossae large and shallow, the ridges confluent with the lambdoidal ridges."

Description. (Plate 3, fig. A-C; Plate 4, fig. A-C; Table 6.1).

No Proc prefrontalis of Os frontale. Cranium and rostrum elongated and dorso-lateral ventrally compressed; main area of elongation (relative to proportions of *Aquila audax* in posterior cranium and nasal regions; line of dorsal surface ± continuous through cranium and premaxilla, with no break or angle as in *Aquila audax.* The principal sites of elongation are anterior and posterior to the orbit; anteriorly, the maxillary process of the nasal is broad and ± equal to depth of internarial bar (it is much narrower in *Aquila audax);* with subparallel sides, and lies at c 30° to the dorsal margin of the rostrum (in *Aquila audax* 45-50°); length of bony nares > 2x height (<2x height in *Aquila audax*). Rostrum elongated towards tip; centre of curvature of dorsal surface at c 0.3-0.5 rostral depth ventral to tomial margin (as against on or dorsal to margin in *Aquila audax*; supranarial ridge swollen - strongly bowed dorsad. Bridge over narial artery and nerve narrow, simple. Temporal fossa deep, postero-ventral angle acute. Ectethmoid plate small, arising ventral to lower margin of nasal arterial foramen, ventral margin horizontal. The nostril aperture is ossified anteriorly, dorsally, and ventrally, forming a partial tube (cf most *Aquila,* but see mounted specimen at OMNZ); remainder of aperture not ossified, cf. *Aegypius* and *Gyps.*

Caudal margin of Proc maxillare Os nasale entire, not notched to receive rostral angle of Os prefrontale as in *Aquila audax.* Tomial margin of Os premaxillare gently sinuate, with the point of maximum depth rostral to rostral margin of nares. Ventral margin of Os palatinum straight for three quarters of distance caudal to tomial margin of Os premaxillare.

Posterior margin of orbit ± straight, at ± 90° to cranial axis, to tip of Proc postorbitalis: in A. audax, there is a broad notch in the rostral margin of Proc postorbitalis. Proc postorbitalis tapers to a blunt point. There is no interorbital foramen. Rear of cranium produced. parietal and supraoccipital regions straight in lateral outline, linked by distinct angles;

Material available. ALBURY PARK, CM, none, B McCulloch, tip of premaxilla, on display, collection of B McCulloch, not measured. AR 144, NMNZ, S 23611pt, includes premaxilla, right jugal bar (complete), palatines (complete), maxillopalatines (complete), left quadratojugal + jugal (broken cleanly from maxillary process), well-preserved. CANNIBAL BAY, S184/4, CM, AV 34466, Les Lockerbie, worn. CASTLE ROCKS, NMNZ, DM 2134pt, A Hamilton, premaxilla tip

broken, no palatines or maxillopalatines. OM, C 40.8, A Hamilton, 1893, includes both jugal bars, R prefrontal, both palatines. ENFIELD?, BMNH, 93.1.30.1, Forbes?, braincase, frontals, interorbital septum: basiparasphenoidal perfect, left postorbital process broken. EAGLE ROOST, NMNZ, S 25580, cranium and premaxilla intact, both prefrontals - right is S 22472.23, left unnumbered, same colour as right, dissimilar to cranium, tympanic margins, basicranium intact, left jugal arch intact, interorbital plate intact. NMNZ, S22473.1, 25 IV 1983, including premaxilla and palatines. GRAVEYARD, NMNZ, S 22712.1, premaxilla tip, beyond Terrace. GRAVEYARD, NMNZ, S 23825pt, May 1987, back to posterior of nares. NMNZ, S 23825pt, May 1987, lacking "upper mandible", damaged braincase + frontal + mesethmoid. NMNZ, S 23825pt, May 1987, premaxilla, back to posterior of nares. HIS & HER, Sq2a, NMNZ, S 23479, premaxilla broken off but present, no palatines. HOLYOAKE STREAM, CM, AV 9554, Ron Henderson, 4 Jan 1945, per Humphrey Belton (Acc Feb 1945), lacking premaxilla etc.; probably from Hawkes Cave, upper reaches of Holyoake Stream, Takaka Hill. MT OWEN, NMNZ, S 27773, D Smith T H Worthy, Jan 1990, complete skeleton. PYRAMID VALLEY, Sq 51, 53, CM, AV 5684, R J Scarlett, 2 Feb 1949, cranium in Sq 51. Sq 68, CM, AV 5685pt, J R Eyles, 15 Mar 1949, was on display, includes left quadrate + jugal bar. NO LOCALITY, NMNZ, DM 2146pt, braincase NOT *H. moorei* - probably albatross.

6.5.8.3 *PREFRONTAL*

Description. (Plate 3, 4, fig. A, B, C). Dorsal surface of Proc supraorbitalis deeply troughed, not planar as in *Aquila*; superciliary free, semielliptical. Anterior angle of corpus not entering notch in Proc maxillare nasale; Proc not notched. Sharp process on rostral margin of Proc orbitalis absent in *Aquila*; process notched at rostral end of flared distal blade; notch absent in *Aquila* where deeply incised caudally. Line of lateral edge of Os prefrontale, when extended caudad, passes just lateral to Proc postorbitalis. Proc supraorbitalis not produced; lateral limb of Incisura ductus nasolacrimalis only marginally longer than medial limb and posterolateral angle of Proc supraorbitalis extends only 0.5x as far laterally from the dorsomedial margin of the orbit as does Proc postorbitalis. In S 27773, posterior margin of Proc supraorbitalis narrower than facies articularis of Ossa supraorbitalia. Ossa supraorbitalia reaches c50% of distance to Proc postorbitalis. Terminal angle of Incisura ductus nasolacrimalis is c60°. Proc. supraorbitalis narrow laterally; incisura ductus nasolacrimalis deep, angled c60° internally; dorsal surface ± deeply troughed antero-posteriorly. Lateral limb of incisura about same length as median, Proc. supraorbitalis not extending caudad far beyond posterior limit of junction between Os prefrontale and Os frontale. In dorsal view, Os prefrontale acutely triangular. Lateral margin thick, dorsal and ventral surfaces parallel, not tapering (narrowing) posteriorly.

Facies articularis supraorbitalis narrower than anterior width of Ossa supraorbitalia. Caudal margin straight, to slightly convex.

Proc. orbitalis slightly bent ventrad distally; tip squared off; lateral facies ending in notch proximally; prominent sharp process on anterior margin mid-way between rostral angle and notch; posterior margin of lateral facies entire, not notched. Rostral margin of corpus with slight internal angle, resulting in rostral angle being acute (c 60°); dorsal margin rostral angle against uninterrupted caudal margin of Proc maxillare of Os nasale, fitting into notch on Proc maxillare. Ossa supraorbitalia articular width > 50% length; in position, posterior margin ±50% distance from posterior margin of Os prefrontale Proc supraorbitalis to Proc postorbitalis. Sides subparallel, gradually narrowing posteriorly.

Material examined. CASTLE ROCKS, OMNZ, C 40.8pt, A Hamilton, 1893, on mounted specimen. EAGLES ROOST, NMNZ, S 25580pt, associated with S 25580 (skull) and S 22472.23 (R prefrontal). NMNZ, S 22472.23, R, associated with S 25580pt (skull) and S 25580pt (L prefrontal). MT OWEN, NMNZ, S 27773pt, L, R, Jan 1990, D Smith, T H Worthy, P R Millener, tomo SO 209. PYRAMID VALLEY, Sq 51 53, CM, AV 5684pt, 1949.

6.5.8.4 *POSTEROPTERYGOID*

Description. (Plate 3, fig. E-I). Proportionately much broader than in *Aquila*: rostral side flange much longer, extending >0.5 caudally. Corpus deeply fluted ventrally; domed dorsally.

Material examined. AR 144, NMNZ, S 23611pt; MOUNT OWEN, NMNZ, S27773pt, L, R, tomo SO 209, parts of complete skeleton.

6.5.8.5 *HYOBRANCHIAL APPARATUS*

Description. (Plate 6, fig. D). Caudal process of Os entoglossum slender. Os basibranchiale rostrale 2x length of Os entoglossum. Os basibranchiale caudale length = length Os entoglossum. Total hyobranchial apparatus length c70% of mandibular ramus length.

Material examined. AR 144, NMNZ, S 23611, lacking both Os basibranchiale caudale. MOUNT OWEN, NMNZ, S 27773, lacking right Os basibranchiale caudale.

6.5.8.6 *QUADRATE*

Description. (Plate 6, fig. E-J). Orbital process compressed, equal in length to otic process; tip of process squared off, as against < otic process and with rounded tip in *Aquila audax.*

Material available. CASTLE ROCKS, NMNZ, DM2134pt, Hamilton. MOUNT OWEN, NMNZ, L, R, S27773pt, SO209. NGAPARA?, OMNZ, C03.61?, Hamilton 1903?. NOLOC, CM, AV9845, No data,. PYRAMID VALLEY, CM, AV5685pt, 1949.

6.5.8.7 *MANDIBLE*

Haast (1881: 233; pl. XIII 1, 2, 3, 4; refers to AV 5323): "From a comparison of the general form of this mandible with that of [*Circus approximans*] it will be seen that it is somewhat narrower in proportion than that of the latter. In this respect it resembles the mandible of [*Vultur gryphus*] and ... *Gyps fulvus.* However, as several others of the vultures have a broad mandible, this character is not of any generic value. But when comparing the shape and size of the articular portion of *Harpagornis* with that of *Circus,* the striking resemblance between both becomes at once manifest. The articular part of the mandible in both is well excavated for the mandibular end of the tympanic bone.

"The articular process has the same form in both. A pneumatic canal perforates the surface of this articular process at its base. The articular depressions for the insertion of the pterygoid muscles and for the two strong ligaments uniting the tympanic and squamosal with the articular part of the mandible are well excavated. The three portions of which the ramus consists when extending forward from the articular end are well cemented together, having a long and well defined articular surface for the insertion of the temporal muscle in the central portion.

"The dentary portion is so well united on the right ramus that its junction with the posterior portion is not well visible, whilst on the left side the separation can be easily traced. From here the dentary curves gradually down to

the symphysis, which is well channelled, measuring .68 inch across the upper portion. A number of nervo-vascular tracts are seen on the anterior part of the symphysis, together with a series of canals on the lower side."

Oliver (1930: 392): "Mandible rather narrow, symphysis channelled."

Oliver (1955: 604): "Mandible rather narrow, symphysis channelled."

Description. (Plate 6, fig. A-C; Table 6.2). Medial articular process with pneumatic foramen. Postarticular process short, subrectangular; at base of medial process. Medial process tapering gradually to point, rostral edge of process ± 90° to axis of ramus; caudal margin curved gently rostrally.

Material examined. CASTLE ROCKS: NMNZ; DM 2134pt; A Hamilton 1893. OM, C40.8, A Hamilton, 1893. ENFIELD?, BMNH, no number visible, Forbes?, heavily varnished, no articular processes. HAMILTON SWAMP 1, CM, AV 5323, B S Booth, Jan 1874, ZFS,686.7, left ramus repaired. AR144, NMNZ, S 23611, perfect. GRAVEYARD 3, NMNZ, S 23825pt, May 1987, left ramus up to symphysis but excluding symphysis. NMNZ, S 23825pt, May 1987, right articulation + part ramus. GRAVEYARD O, NMNZ, S 22765, lacking R articulation, L ramus worn. HIS & HER, NMNZ, S 23480, symphysis only. NMNZ, S 23480pt, symphysis only. MARFELL BEACH, CM, AV 12152, R J Scarlett, Jul 1952, symphysis + stubs of rami. MOUNT OWEN, NMNZ, S 27773, Jan 1990, see cranium same number, part of complete skeleton. PYRAMID VALLEY, Sq68, CM, AV 5685pt, J R Eyles, 15 Mar 1949, associated with cranium. Sq VII, CM, AV 12355, Canterbury Museum party, 12 Feb 1939.

6.5.8.8 *VERTEBRAE*

Description. (Plate 5, fig. A-F; 7, fig. A-D; 8, fig. A-C; 9, fig. A-D). Vertebrae typical of accipitrids (see Pycraft 1902), except for great dorso-ventral depth of thoracic series, and size of notches for nerve roots passing to the wings and legs (Plate 8).

Material available. CASTLE ROCKS, OMNZ, C 40.8pt, A Hamilton, 1892-3, x cervical (x belonging to individual under DM 2134), x thoracic (x belonging to individual under DM 2134), x caudal (x belonging to individual under DM 2134). GLENMARK, CM, AV 5327, no data. AR 144 L2, NMNZ, S 23611pt, 4. EAGLE ROOST, NMNZ, S 22472.19. EAGLE ROOST 4, NMNZ, S 23001.2, P R Millener, 25 Apr 1983, behind G, P.W. excav, Bay 4. EAGLE ROOST H, NMNZ, S 22472.22. NMNZ, S 22472.20. NMNZ, S 22472pt. NMNZ, S 22472.18. NMNZ, S 22472.21. HIS & HER, Worthy coll., none, T H Worthy, 3 Jul 1990, attributed by T H Worthy, not confirmed. KINGS CAVE, CM, AV 24783pt, Canterbury Caving Club, 7th? cervical, 8 Aug 1970, mud, higher level. MARFELLS BEACH, CM, AV 16329, 1 thoracic (possibly not *H. moorei*), 3 Jul 1956, J & R Britton. MT OWEN (SO209), NMNZ, S 27773pt, 11 cervical, 8 thoracic, 6 caudal. OAMARU/WANBROW, AU, AU 9723pt 4, P R Millener J A Grant-Mackie, possibly *H. moorei*.

OLD RIFLE BUTTS/Loc D, CM, AV 24887pt, 1st presacral thoracic, R J Scarlett, 1-2 Sep 1970. PYRAMID VALLEY, Sq 68, CM, AV 5685pt, 15 Mar 1949. CM, AV 5685pt, 4th cervical, 15 Mar 1949. 68, CM, AV 5685pt, 7th? cervical, 15 Mar 1949.

6.5.8.9 *RIB*

(Haast 1872: 194; pl. XI 5): "Another bone which belongs to the same species is a rib. It is the third rib on the right side, the first after the pleurophyses or two floating ribs, and articulates with the haemapophysis or sternal rib, and through the latter bone with the sternum. Pl XI, fig. 5, represents in natural size this well preserved bone, of which only at b the upper portion of the epipleural appendage is broken off. The coalescence of this latter portion of that bone, which is a well marked peculiarity of raptorial birds, is well shown in this specimen, thus offering additional evidence as to the specific character of the specimen under review.

Description. Uncinate processes large, on complete thoracics x-x.

Material available. NO LOCALITY, NMNZ, DM2146pt, ?, no data.CASTLE ROCKS, OMNZ, C 40.8pt, 11 L, 6R, A Hamilton. NMNZ, DM2134pts, B, A Hamilton. AR 144 L2, NMNZ, S 23611pt, ?. NMNZ, S 23611pt, ?. NMNZ, S 23611pt, ?. NMNZ, S 23611pt, ?. NMNZ, S 23611pt, ?. NMNZ, S 23611pt, ?. NMNZ, S 23611pt, ?. EAGLE ROOST H, NMNZ, S 22472pt, ?. NMNZ, S 22472pt, ?. MT OWEN (SO 209), NMNZ, S 27773pt, 12L, 11R. NOLOC, NMNZ, DM2146pt, ?. OLD RIFLE BUTTS Loc D, CM, AV 24887pt, ?, R J Scarlett, 1-2 Sep 1970.

6.5.8.10 *STERNUM*

Hamilton (1894: p. XXIII 2, 3, 4; Scarlett (1972: fig. 144, 145, 146, 147)

Oliver (1930: 392): "Sternum with deeply convex body and high rounded keel; coracoid grooves meeting in front, lateral processes small; six costal articular surfaces; xiphisternal border with a shallow notch and a fenestra (often incomplete) on each side."

Oliver (1945: 137): "The sternum had a broad notch on either side, a character that may be regarded as a little primitive."

Oliver (1955: 604): "Sternum with deeply convex body and high rounded keel; coracoid grooves meeting in front, precostals small; six costal articular surfaces; xiphisternal border with a shallow notch and a foramen (often incomplete) on each side."

Description. (Plate 10, fig. A-B; Table 6.3). Carina, deepest part anterior, as in *Aquila*, not further back, as in *Gyps* or *Aegypius*: thicker than in *Gyps* or *Aegypius*; pila carina especially thick, as in *Aquila*. Bowl of sternum hardly extending ventrally down keel (cf. *Aegypius, Gyps,* where keel narrowed by bowl). Costal margin 0.5-0.66 of anterior margin. Ventral margin of coracoidal sulcus more posterior in *Harpagornis* than in *Aquila*; obscuring dorsal margin in ventral view in *Aquila,* not in *Harpagornis.* In dorsal aspect, anterior pillar visible inside bowl as flat-topped ridge, with lateral furrows; not so in *Aquila*. Six costal articulations, coracoidal sulcus reaching to 4th. Spina externa deeper than broad in *Harpagornis,* narrower in *Aquila.*

Material available. NO LOCALITY, CM, AV 15965, "Faint trace of writing looks like von Haast's", fragment of posterior with carina. CASTLE ROCKS, NMNZ, DM 2134pt, A Hamilton, 1893, from "lateral arm" of the fissure (F, see Fig. 8.4B), "At the very end, firmly fixed in the hard carbonate of lime". OM, C 40.8, A Hamilton, 1893. ENFIELD?, BMNH, none, H O Forbes?, 1891/2, manubrium + most of coracoidal sulci and anterior section of keel. EAGLE ROOST G, NMNZ, S 22473.2, carina broken away caudally. NMNZ, S 22473.3, with calcite encrustation. GRAVEYARD/Terrace 2, NMNZ, S 23051.1, T H Worthy, from site 3 (T H Worthy 1987) and (anterior section only) equates to S 23030. MT OWEN, NMNZ, S 27773, Jan 1990, part of complete skeleton. NGAPARA, OM, C03.61pt, A Hamilton, 1903, fragment. NGAPARA?, OMNZ, A/3, C23.29?, A G Gilkison?, 1932?, 1923?, fragment of R anterior of sternum + posterior end of keel. OLD RIFLE BUTTS, CM, AV 24887pt, R J Scarlett, 1-2 Sep 1970, fragments. PYRAMID VALLEY, Sq 54, CM, AV 6012, J R Eyles R J Scarlett, 5 Feb 1949, 5 fragments, part of AV 6177 (2 parts). Sqs 84 & 66: CM, AV 6177pt, Sq 84, 2 Apr 1949, Sq 66, 8 Mar 1949, J R Eyles R J Scarlett, fragments of 1 sternum - associated 18 Oct 1951, R J Scarlett.

6.5.8.11 *PELVIS*

Haast (1874: 72, measurements; 71-75, description; pl. IX, 1, 2, 3): "This compound bone, ..., has all the characteristics which belong to the pelvis of a diurnal raptorial bird, some of the complex features, owing to its enormous size, being developed in a most remarkable degree. It combines great strength with lightness and elegance of form, of which the drawings attached to this memoir will convey an accurate description better than words can do. In comparing the pelvis of *H. moorei* with those of *Aquila audax,* ..., and of *Circus assimilis* [=*C. approximans,*] ..., and *Hieracidea novae zealandiae* [=*Falco novaeseelandiae],* ..., the striking difference in size becomes at once manifest. When examining [the] table of measurements another peculiar feature of the fossil bone [is] its great length when compared with its breadth; whilst in the three recent species the

double breadth is more than the length, in *Harpagornis* it is considerably less. This peculiarity is produced principally by the greater steepness of the pelvic roof and by the comparatively greater length of the ilio-ischial plates; moreover it is also higher in proportion than any of the recent species of Diurnal Raptores with which I could compare it.

"When viewed from below the space formed by the hind part of the neurapophysial crest and the two ilia has an oval shape; whereas in the three recent species ... it is shorter, more open, and semi-circular.

"Beginning with the first sacral vertebra, ... the articular surface of its centrum is broader in a transverse than in a vertical direction, 0.69 inch by 0.58 inch. The neural canal has an oval form, its largest diameter, 0.21 inch, being in the vertical line in this respect resembling *Circus;* whilst in *Aquila,* and still more in *Hieracidea,* the canal approaches the circular form.

"The prezygapophyses are of middle size and stand forward, their articular surface of a rounded shape, being almost plane. the neural spine is broad and strong at its base, gradually contracting, and forming only near its coalescence a small neurapophysial expansion lying between the iliac plates.

"A broad and deep ilio-neural opening is formed on each side of the spinal plate, having a greater vertical than lateral extent, and here again differing from the pelvis of the three recent species ..., the roof framed by the iliac plates of *Harpagornis* being consequently considerably steeper.

"The surfaces for the head of the two free sacral ribs are strongly developed, the iliac roof extending, however, a little beyond them.

"The under surface of the first sacral centrum in its anterior portion is slightly carinate, whilst the centres of the two succeeding ones are rounded, the edges of their articular surfaces being well raised, the posterior one of the third centre the least; after which they flatten and expand to the beginning of the interacetabular region, contracting again to its termination, and possessing a transversely concave, shallow, inferior surface, being broadest near the anterior articular surface of the seventh vertebra.

"From the eleventh to the fourteenth they still diminish in breadth, and now exhibit a low but well marked inferior ridge, running out before the last sacral vertebra is reached.

"The parapophyses of the third to the sixth sacral vertebra are anchylosed to the lower border of the ilia, forming four interapophysial vacuities on both sides; of these the last parapophysis is the strongest and thickest, standing at right angles to the direction of the axis of the vertebral column.

"There is a short parapophysial process starting from the seventh vertebra (the first of the four next vertebrae forming the interacetabular region), which has a downward direction, and is still attached on the left side of the pelvis to the inner edge of the head of the pubic bone.

"In the pelvis of *Harpagornis assimilis* this process does not exist, and it resembles in this respect the recent species previously used for comparison. Of the parapophyses of the last four vertebrae, forming the postacetabular region, the first one belonging to the eleventh sacral centrum is a filamentary bone joining the second round and strongest parapophysis, which abuts against the innominate, and with which the posterior ones are also connected by their distal ends.

"Of the interapophysial vacuities the first, second, and fourth are elongate, whilst the third and largest is more circular. In the smaller pelvis of *Harpagornis assimilis* these vacuities are not relatively, but actually, larger than that in *H. moorei*.

"The coalesced distal portion of these parapophyses runs in an oblique angle from the inner region of the ilia to the abutment of the twelfth sacral centrum, the space between this distal line and the upper side of the ischiadic foramen, below the pelvic disk, being spanned over by a thin deck of bone, perforated by a large oval opening 0.48 inch in its largest diameter, which runs parallel to the main axis of the pelvis, and is situated on each side behind the upper and anterior wall of the ischiadic foramen.

"The last sacral vertebra of *H. moorei* is not yet quite anchylosed to the foregoing vertebra, thus shewing that it belonged to a not quite adult individual; on the other hand, in the pelvis of *H. assimilis* the articular surfaces of these two

last vertebrae are well anchylosed, and the junction of the parapophyses with the lower border of the ilia in its antacetabular part is also well accomplished, which is not quite the case in the pelvis of the larger species ..., so that we may safely assume that the former belonged to a full-grown mature specimen.

"The gluteal ridge is decayed in *H. moorei*, but is well developed and preserved in the smaller species, the gluteal process forming a rounded knob, which rises well above the pelvic disk, whilst in *Aquila* this process has a convex form, directed downwards, and standing well in advance of the ilia. Of the recent species *Circus* resembles most, in this respect, the extinct gigantic form.

"The pre-acetabular iliac plates unite about one-third from their anterior end above the summit of the sacral ridge, diverging again after having been united for 1.70 inch to form a small interposed neural expansion, anteriorly lying scarcely below the upper border of the iliac plates. In this respect it resembles *Aquila,* whilst in *Hieracidea,* and still more in *Circus,* the neural interposition is continuous all the way, but is narrowest in the region where, as observed, the iliac pre-acetabular plates meet in *Harpagornis.*

"The ischium is very strongly developed at the back part of the acetabulum, as might be expected in a bird of such great strength. The tuberosity of the ischium, a roundish flat process, 0.72 inch from its posterior termination, rises conspicuously above its lamelliform surface. The posterior termination of the coalesced ischium and ilium is not rounded off, as in *Aquila,* but has a rather acute form, which, of recent species, *Circus,* and still more conspicuously *Hieracidea,* also possess.

"The pubic bone, after having formed the lower boundary of the obdurator notch, gradually loses its trihedral shape and assumes a vertically flattened form, continuing to run for some distance parallel with the ischium; however, as in both specimens its posterior portion is broken off, I cannot say how far it may have extended. In any case it is longer then in *Aquila.*

"A thin plate of bone, closely connected with the lower border of the ischium and gradually thickening, runs to the termination of that latter bone. At its beginning it forms the posterior boundary of the obdurator foramen, and fills up the space between the ischium and the pubic bone.

"The subacetabular fossae, which are very shallow in *Aquila* and the Diurnal Raptores now living in New Zealand, are deeply excavated. The pelvic disk is a strong bone separated on each side by a well-marked line from the hind part of the neurapophysial crest, which rises well above it, the latter showing, like all the rest of the bones of which the pelvis is formed, a remarkable development of all the principal features to be observed in the pelvis of the smaller recent Diurnal Raptores.

"Finally, I wish to observe that the pelvis of *Harpagornis moorei,* from Otago, has still some of its integuments and ligaments attached, of which the lining membrane on the walls of the acetabulum are best preserved; . . ."

Owen (1879: 143-145; pl. CV 1, 2, 3): "The... pelvis is characterized by the great proportional extent of its ant-acetabular part, by the depth, strong definition, and muscular sculpturing of the surface of the ectiliac fossae, by the breadth of the iliosacral disk, by the depth and strength of the ischia between the ischiadic and obdurator foramina, and by the close connexion of the pubis with the ischium beyond or behind the obdurator foramen. The conformity of the pelvis with that of our Blue Harrier in the foregoing characters will be obvious in comparing fig.1 with fig. 7, both of the natural size; but the difference in relative vertical extent if ilium and ischium, and relative size of the foramen is to be noted. The parapophyses of the six anterior sacral vertebrae abut against the ilia near the lower border of those bones. Below this abutment the first and second vertebrae develop the cups for the tubercles of the last two pairs of movable ribs; the cups for the heads of these ribs are on the centrum, below the origins of the parapophyses. These processes in the four following sacrals have coalesced with the ilia. Of the interapophysial vacuities the first and second are the largest, the three smaller ones are subequal.

"Four interacetabular sacrals, in which the parapophyses are suppressed to give space to the praerenal lobes, are followed by four postacetabular sacrals, in which the parapophyses are resumed. Of these the first pair are slender, the second and third suddenly expanded, the latter apparently bifurcate; the fourth pair are short, and inclined backward; on each side of the sacrum these parapophyses coalesce with each other and with the ilia at their outer ends. The

last sacral vertebra has not coalesced with the preceding, but appears the have been closely joined therewith, as the ends of its short and thick parapophyses combine with those of the fourteenth sacral to abut against the inflected parts of the ilio-ischial deck-like process. In the number of sacral vertebrae (fifteen) *Harpagornis* agrees with *Falco* and *Circus,* and differs from *Aquila;* in the species of which I have examined the pelvis there are but fourteen sacral vertebrae. The ischiadic foramen extends relatively further beyond the postacetabular facet in *Harpagornis* than in *Aquila;* the foramen is relatively less than in *Circus.*

"The praerenal or interacetabular fossae are relatively narrower in *Harpagornis* than in *Aquila* or *Circus,* and more resemble those in *Buteo.* The pubic portion of the acetabulum does not extend so far outward as in *Aquila. Buteo vulgaris* and *Falco communis,* as well as *Circus gouldi* and *Circus cyaneus,* resemble *Harpagornis* in the vertically oval figure of the anterior orifice of the neural canal; in the smaller species (*Circus pygargus,* the Ring-tail or Montagu's Harrier) this outlet is circular, as in most species of *Aquila.* The iliac roofs of the long acetabular division of the pelvis are steeper in their slope than in *Circus* and most Eagles; the ilio-neural openings have consequently, as Dr. Haast has remarked, "a greater vertical than lateral extent." The gluteal processes appear to have been broken of in the fossil; they are more strongly developed in *Circus* and *Buteo* than in *Aquila.* Both first and second sacral vertebrae have well-defined articular surfaces for the head of a rib; and there are indications of a surface for ligamentous attachment of a third free or movable pleurapophysis in the pelvis of *Harpagornis.* The extremity of the long and slender pubis has been broken off in the fossil; but doubtless it had similar proportions when entire, to that element of the pelvis in most existing diurnal Raptorial birds."

Oliver (1930: 392): "Length of pelvis more than twice breadth; preacetabular plates united above but diverging in front and behind; ischia strongly developed and expanded, pointed posteriorly."

Oliver (1945: 137): "In the pelvis the escutcheon widens abruptly both in front and behind, thus differing from the usual eagle type."

Oliver (1955: 604): "Pelvis with ilia united above but diverging in front and behind; ischia strongly developed and expanded, pointed posteriorly."

Description. (Plate 10, fig. C-E; Table 6.4) Pre-postacetabular angle steeper than in *Aquila*. Ilio-ischiadic foramen produced postero-dorsally to make 'rounded triangle', oval in *Aquila*; pit in ischial bar, immediately posterior to acetabulum; anterior iliac plates produced dorsally above synsacrum, leaving deep dorsal bowl, ± flat in *Aquila*; dorsal surface extends posterior to posterior edge of ilio-ischiadic foramen: anterior to (c 50%) in *Harpagornis* and *Aquila,* visible in lateral view in vultures. Posterior superior iliac plates extend laterally past the antitrochanter. Fused caudals 2+2 as in *Aquila;* 2+3 in *Gyps* and *Aegypius*. Ratio of height to width at highest point of anterior ilium 51:42.5, as against 29:30 in *Aquila,* 42.5:47.5 in *Aegypius*, and 40:54 in *Gyps*. In *Gyps,* posterior border of ilio-ischiadic plate with large notch; obscure in *Aegypius*, convex (slightly) in *Harpagornis* and *Aquila.* Highest point of anterior iliac crest c30% back in *Harpagornis,* c50% back and flat in *Aquila,* anterior in vultures. Antitrochanter ± rectangular (slightly narrowing posteriorly) in *Harpagornis,* tapering more in *Aquila;* ± triangular in *Aegypius*, ± rectangular in *Gyps*.

Material examined. "NELSON", CM, AV5332, CAST. CASTLE ROCKS, NMNZ, DM2134pt, A Hamilton, 1891/2, 6 synsacral vert, fused caudal formula 2+2. OM, C40.8, A Hamilton, 1893. GLENMARK/ EAST SIDE, CM, AV5102pt, Haast party 1873, part of *H. assimilis* type series (see Fig. 6.2). HONEYCOMB/ EAGLE ROOST G, NMNZ, S22473.4. NMNZ, S22473.5, broken cranially. HONEYCOMB/ GRAVEYARD L3 EX 1, NMNZ, S23664pt, T H Worthy, Feb 1987, synsacrum only. NMNZ, S23030pt. HIS & HER, NMNZ, S23460, fragmentary. NMNZ, S23461, 5 pieces, ischium etc. MT OWEN, NMNZ, S27773, Jan 1990, complete skeleton. OAMERU = ENFIELD, BMNH, A424, H O Forbes, sacrum + pelvis, Pleistocene. OBELISK RANGE/ COWES, BMNH, 75.12.15.34, W A Low, to NMNZ with moa bones (+ others?), then with Hector to UK, perfect, with remains of ligaments on internal inferior process of acetabulum, slightly abraded on anterior iliac crests, synsacral caudal processes perfect, 2+2 = (split + 1) + 2.

6.5.8.12 *CORACOID*

Scarlett (1972: fig. 131).

Description. (Plate 11, fig. C-D; Table 6.5). Lateral angle between scapula and coracoid when articulated more acute in *Harpagornis* than in *Gyps*; prominent triangular bulge on dorsal surface of coracoid for major sternal ligament, more sternal and lateral in *Gyps*, not raised in *Aquila.* Procoracoid prominent; procoracoidal foramen present. Scapular facet oval, long axis crosswise. Procoracoid not deflected at tip as in vultures. Circular pneumatic fossa in

triosseal canal, beneath brachial tuberosity; foramina small to minute; rectangular fossa within fossa. Sternocoracoidal process long, blunt, rounded sternally. Deep fossa ventral to glenoid facet; bicipital attachment with pits laterally and ventrally.

Material examined. LOCALITY UNKNOWN: CM, AV5339, R, broken and repaired. NMNZ, DM2146pt, R. "OTAGO"=ENFIELD?, CM, AV5334, R, CAST. CASTLE ROCKS, OM, C40.8, L, R, A Hamilton, 1892. NMNZ, DM2134pt, R, A Hamilton, 1891/2, second coracoid found in 1891 (first was, from measurements, right of C40.8). ENFIELD?, BMNH, 3, L, ?Forbes, 1891, worn. BMNH, 4, R, ?Forbes, 1891. AR144, NMNZ, S23611pt, L, HONEYCOMB/ EAGLE ROOST H, NMNZ, S22472.2, L, P R Millener, 26 Oct 1982, abraded cranially. NMNZ, S22472.3, R, P R Millener, 26 Oct 1982. HONEYCOMB/GRAVEYARD: NMNZ, S22653pt, L, 4 Apr 1983, not from same bird as S22653 R. NMNZ, S22653pt, R, 4 Apr 1983. HIS & HER, NMNZ, S23451, L, T H Worthy. NMNZ, S23452, L, T H Worthy. No number, T H Worthy coll, L, T H Worthy, 3 Jul 1990, parts of humeral end only (paired with R element from same site). NMNZ, S23453, R, T H Worthy. No number, T H Worthy coll, R, T H Worthy, 3 Jul 1990, recovered from His & Her excavation debris. MARFELLS BEACH, CM, AV13014, L, R J Scarlett, Jul 1952. MT OWEN, NMNZ, S27773, L, R, Jan 1990, parts of complete skeleton. NGAPARA, OM, C32.82, L, A G Gilkison, not found 24 Jul 87. NGAPARA?, OMNZ, unnumbered, L, A G Gilkison 1932? not seen 24 Jul 87, in new box 10 Jul 90, sternocoracoid process damaged. Shirley Creek/ Cape Wanbrow, NOM, Bruce McCulloch 1979, details per Bruce McCulloch.

6.5.8.13 *SCAPULA* Scarlett (1972: fig. 68)

Description. (Plate 11, fig. A-B; Table 6.6). Neck long (c25% total length). Dorsal margin of blade ± in line with neck; angle in blade quite sharp, c30°; caudal margin convex. Large pneumatic foramen beneath acromion; acromion broad, horizontal, foramen under medial ledge. Coracoidal articulation ovoid, long axis at c90° to line of acromion edge. Small foramina on medial side of coracoidal facet.

Material available. CASTLE ROCKS, NMNZ, DM2134pt, L, R, A Hamilton, 1891/92. OM, C40.8, L, R, A Hamilton, 1892. ENFIELD?, BMNH, 6, L, Forbes, 1891. BMNH, none, R, Forbes, 1891. GLENMARK/EAST, none, L, Haast party, 1873, listed by Haast (1874) as from *Harpagornis assimilis*, i.e. part of AV 5102, not listed as such now in Accession register, therefore missing before R J Scarlett compiled AV index in 1950. GLENMARK/WEST, CM, AV 5104pt, L, R (deformed), Haast party, 1873. HAMILTON SWAMP, AIM, 574pt, ?, B S Booth?. GRAVEYARD/terrace, NMNZ, S 23051.2, L. HIS & HER, NMNZ, S 23448, L, T H Worthy, proximal end. NMNZ, S 23449, L, T H Worthy, proximal end. NMNZ, S 23446, R, worn proximally, and part of blade. NMNZ, S 23447, R, T H Worthy, proximal (=cranial) end. MT OWEN, NMNZ, S 27773, L, R, D Smith T H Worthy P R Millener, Jan 1990, parts of complete skeleton. NGAPARA?, OMNZ, A/4, C23.29?, R, A G Gilkison?, 1923?, 1932?, lacks blade. OARO, CM, AV5333pt, L, O B Stanford, 1937. OLD RIFLE BUTTS, CM, AV 24887pt, R, R J Scarlett, 1-2 Sep 1970, noted as L in original book list, worn distally. GRAVEYARD 1/L3, NMNZ, S 23664pt, NOT *HARPAGORNIS MOOREI* - fragment.

6.5.8.14 *FURCULA*

Description. (Plate 11, fig. E-F; Table 6.7). Anterior edge of blade straight on ramus, then curving full 90°; two grooves in scapular facet; scapula tuberosity blunt.

Material available. NO LOCALITY, NMNZ, DM2146pt, left clavicle, articulation and blade. "OTAGO"= ENFIELD?, CM, AV 5335, CAST. BMNH, 4?, Forbes?, 1891, dorsal sections of both rami. CASTLE ROCKS, OM, C 40.8, A Hamilton, 1893. NMNZ, DM 2134pt, A Hamilton, 1891, R + symphysis, in Hamilton (1893) noted as having been broken with a pick, and lost remaining portion. AR 144, NMNZ, S 23611pt, complete, broken cleanly and repaired. EAGLE ROOST H, NMNZ, S 22472.1, P R Millener, 26 Oct 1982, perfect. GRAVEYARD 1, NMNZ, S 23720pt, symphysis only. GRAVEYARD 3, NMNZ, S 23825pt, May 1987, right ramus complete, short section of left. HIS & HER, NMNZ, S 23450, "bow" only. OLD RIFLE BUTTS, CM, AV 24887pt, R J Scarlett, 1-2 Sep, 1970, frag. OREPUKI, SOUTH, none, Alex King, 1945-46, apparently complete, measured by Michael Forrest (letter 1 Jun 1989).

6.5.8.15 *HUMERUS*

Haast (1874: 64, measurement; 69-70, description; pl. VIII, 1, 2): "shaft not so straight as that of *Aquila*, having below the lower termination of the radial crest an outward bend, which is also well exhibited in *Circus*. At the same time, the proximal extremity is more curved towards the ulnar side...; shaft at one-third of its total length above its distal end is nearly round in a transverse section, a feature it has in common with *Circus*, whereas the shaft of *Aquila* is more subelliptic. The articular head forms a more distinct tuberosity than in *Aquila*, which is also observable in *Circus*; a broad groove dividing it from the ulnar crest, which advances considerably over the pneumatic foramen. The radical crest being partly broken off, its whole extent cannot be ascertained. The ridge forming the boundary of the large depression for the insertion of the pectoralis major is well marked. The articular convexities of the distal extremities are also of considerable size, and well carved out; the pits for the attachment of the muscles are large and deep, . . ."

Owen (1879: 145, pl. CVI, 1, 2): "This bone appears ... to have lost the terminal angle of the projecting crest called 'pectoral' or 'delto-pectoral:' it is restored in dotted outline after the type of that in *Buteo* and *Circus*. The slight outward bend of the shaft beyond or below this process, which distinguishes the great wing-bone in the Buzzards, Falcons, and Harriers from that in the Eagles,

is well shown in the photographs, and is noticed by Dr. Haast in the original bone. The articular head is transversely broader, in proportion to the fore-and-aft diameter, in both the extinct *Harpagornis* and in existing Falcons than in Eagles. The pneumatic ridge or crest, extending from the ulnar tuberosity to below the pneumatic orifice, is relatively shorter in *Harpagornis moorei* than in *Aquila chrysaetos*; the breadth of the entire proximal end is relatively greater in the Falcons than in the Eagles. The radial tuberosity is more strongly marked in *Harpagornis moorei*. In this huge species the graceful sigmoid bend of the entire humerus is better marked than in the smaller existing Falconines and than in any Eagle; it suggests a greater force in the movements of the wing. The longitudinal line along the palmar aspect of the shaft is better marked in *Harpagornis moorei* than in the humerus of any existing Raptorial species, though not so developed as to be termed a ridge. In this character the Falcons make the nearest approach to their great extinct confamiliar. In both the line rises to the character of a ridge as it descends to terminate in the palmar prominence of the ulnar epicondyle. The radial epicondylar prominence is characteristically developed in both the recent and extinct Falconines. The condyles themselves show the usual well-marked modification of that part of the humerus in birds of flight. The radial and ulnar convexities are strongly marked in *Harpagornis moorei*. The least circumference of the shaft of the present humerus is 2 inches 2 lines; it formed part of the series of the smaller (male?) *Harpagornis* (*H. assimilis*, Von Haast), and is estimated to have been one inch shorter than the humerus in the female (?*H. moorei*, Von Haast), of which the shaft only was found.

Scarlett (1972: fig. 12).

Description. (Plate 11; fig. G-H; Table 6.8). Bone stout, shaft with strong sigmoid curvature in antero-posterior plane; capital groove broad, deep, pierced by small pneumatic foramina; internal tuberosity large, with distinct pit on dorsal surface; infraspinatus attachment long, crescentic; bicipital surface planar; pneumatic fossa short, broad; median crest reaching distal end of bicipital crest; supraspinatus scar dorsal to median crest; nutrient foramen with distinct groove, 2/3 way distally along distal edge of deltoid crest; bicipital crest equidistant from head to nutrient foramen, narrow, thick, joining clear intermuscular line away

from posteromedial margin of shaft; angle between distal margin of bicipital crest and shaft axis c90°; bicipital surface subtriangular; external tuberosity flat, ± diamond-shaped; ligamental furrow interrupted by ridge linking head and bicipital surface, medial section deeply excavated, subrectangular, lateral (dorsal) section shallow, crescentic; latissimus dorsi posterioris offset from, and at angle to, line of latissimus dorsi anterioris, this itself parallel to posterocaudal margin of shaft for 2/3 of length then cranially at c15°; dorsal surface of pneumatic fossa with pneumatic foramina for < 1/2 width of fossa; deltoid crest large, strongly curving dorsad, cranial margins subequal in length, distal margin straight, not running directly into margin of shaft but with step; distal end <1/2 >1/3 way along shaft; midpoint of shaft subrectangular in section; brachialis anticus impression occupying most of brachial depression, rugose; tricipital grooves weakly demarcated, especially external; external surface of ectepicondyle with double pit; entepicondyle extending proximally half length of ectepicondyle; pronator brevis attachment dorsal to anterior articular ligament scar; entepicondyle with double pit. Internal condyle subtriangular, separated from external condyle by narrow deep, groove; dorsal margin of external condyle at c45° to axis of shaft.

Material examined. NO LOCALITY: NMNZ, DM2146pt, R, no data. "PYRAMID VALLEY", CM, AV5587, L (dist + shaft), no data. ALBURY PARK, CM, none, L, B McCulloch, collection of B McCulloch, on display Canterbury Museum, not measured. CASTLE ROCKS, OM, C40.8, L, R, A Hamilton, 1893. CASTLE ROCKS?, NMNZ, DM2145pt, L, same length as L hum collected by A Hamilton at Castle Rocks which has not been identified as such elsewhere. ENFIELD?, BMNH, 8, L, Forbes?. BMNH, 9, R, Forbes?. OAMARU [=ENFIELD], BMNH, A423, L, presented H O Forbes 1894. GLENMARK CREEK, CM, AV9556, R (shaft), "1873", mentioned in Haast (1872), collected c1871. GLENMARK/ EAST SIDE, CM, AV5102pt, R, Haast party 1873, part of *H. assimilis* type series. HONEYCOMB HILL CAVE/ HIVES PASSAGE, CM, AV36396, R, M M Trotter, P Wood et al. HONEYCOMB HILL CAVE/ 'E' ENTRANCE, NMNZ, S25877, L, shaft only, in stream passage which flows beneath Entrance E. HONEYCOMB HILL CAVE/ EAGLES ROOST, NMNZ, S25581, R, associated with S22472. HONEYCOMB HILL CAVE/ EAGLES ROOST ROCKFALL L, NMNZ, S22736, L, P R Millener, Jul 1982. HONEYCOMB HILL CAVE/ GRAVEYARD LEVEL 3, NMNZ, S23030pt, L. NMNZ, S23825pt, L, May 1987, deltoid crest worn, distal end worn. NMNZ, S23825pt, R, May 1987. NMNZ, S23825pt, L, May 1987, good condition. NMNZ, S23825pt, R, May 1987, shaft + pt distal end. HIS & HER CAVE, NMNZ, S23431, L, T H Worthy. NMNZ, S23432, L, T H Worthy, broken, repaired. NMNZ, S23433, L, T H Worthy, broken, repaired, distal end worn. NMNZ, S23459pt, L, distal, incl part of shaft with end of deltoid crest. NMNZ, S23459pta, L, 3 frags - shaft + prox section, larger than more complete R under same number WD 31.5++. NMNZ, S23459pt, R, distal section + pt of proximal shaft with end of deltoid crest. NMNZ, S23459ptb, R, smaller than L (3 frags) with same number. HONEYCOMB HILL/ UNIT HOLE, CM, AV36008, L (dist,

shaft, pt prox), R (shaft), P Wood, 24 Oct 1980. KAKANUI BEACH, CM, AV29361pt, L (worn), washed from bank by high tides, J Park per Cyril [illegible], Oct 1974. MOTUNAU, NMNZ, DM2143pt, L, A McKay, 1881, with moa bones. MT OWEN, NMNZ, S27773, L, R, Jan 1990, D Smith, T H Worthy, P R Millener, parts of complete skeleton. NGAPARA?, OMNZ, A1, C23.29?, R, A G Gilkison 1932?, proximal part only. OARO, CM, AV5333pt, L, R (prox missing), O B Stanford 1937.

6.5.8.16 *ULNA*

Haast (1874: 70, measurements; 70-71, description; pl. VIII, 3, 4): "In comparing its total length with the corresponding bone in *Aquila audax*, ..., it will be seen that it is only 0.68 inch longer, but that it is distinguished from it by its considerable thickness and the greater expansion of both articular ends. This is most conspicuous when examining the proximal surface, but, considering the great breadth of the distal end of the humerus, quite a natural consequence. The anconal side of the shaft is rather flatter than in *Aquila*, so that the bone does not exhibit quite such a great curve as the latter. The quill knobs are obliterated.

"... when compared with *Aquila audax*, ... this ulna, being actually shorter than the corresponding bone of the Australian species, it is much [shorter, as published; the University of Canterbury copy has been changed, in pencil, to "stouter", in Hutton's hand] in all its proportions. The two rows of quill knobs, and principally the one on the palmar side, are well seen, as well as the intermuscular ridge on the palmar side, and the flat processes for the attachment of the muscles."

Owen (1879: 146, pl. CVI, 3): "The ulna is distinguished from that of the largest Eagles more by its thickness and the expansion of its articular ends than by its superiority in length. The proximal surfaces for both condyles of the humerus bear proportion to their characteristic development in that bone; the 'coronoid' angle is well marked. The distal articular convexity indicates the extent of the evolutions of the manual part of the wing, with its great 'primary remiges,' in the action of flight."

Scarlett (1972: fig. 39).

Description. (Plate 12, fig. A-B; Table 6.9) External cotyla with distal flange extending to 0.5x way along proximal radial depression. Bicipital attachment level with end of prominence for anterior articular ligament. Impression of brachialis

anticus to >25% shaft length. Nutrient foramen c33% along shaft. Tricipital attachment ovoid, at level of 'highest' point of internal cotyla. Olecranon blunt, grooved. Thirteen or fourteen obvious secondary papillae. Carpal tuberosity large. Tendinal pit rectangular, groove narrow.

Material available. CASTLE ROCKS, NMNZ, DM 2134pt, L, olecranon worn, R, perfect, A Hamilton. OM, C 40.8, L, R, A Hamilton, 1893. ENFIELD, CM, AV 5329pt, L, P H & H O Forbes. ENFIELD?, BMNH, 12, L, Forbes?. ENFIELD?, BMNH, 13, R, Forbes?. GLENMARK/EAST, CM, AV 5102pt, L, R, Haast party, 1873, parts of *Harpagornis assimilis* type series. GLENMARK/WEST, CM, AV 5104pt, L, worn proximally, R, Haast party, 1873. HAMILTON, OMNZ, unnumbered, L, Hutton & Booth, 1874, 22.4 refers to distal dimension across curves. CM, AV 5324pt, R, B S Booth, Jan 1874. CM, AV 9555, R, B S Booth, Jan 1874, shaft. AR144, NMNZ, S 23611pt, L. NMNZ, S 23611pt, R, proximal section only. HIVES, CM, AV 36405, L, M M Trotter Philip Wood, 23-26, Oct 1981. EAGLE ROOST H, NMNZ, S 22472.6, L, P R Millener, 26 Oct 1982, perfect. GRAVEYARD 1, NMNZ, S 23664pt, ?, L?, proximal shaft (probably ulna), smaller than R? with same number. GRAVEYARD 3, NMNZ, S 23030pt, R. GRAVEYARD 3, NMNZ, S 23825pt, R, May 1987, proximal part missing, distal end damaged. GRAVEYARD 3, NMNZ, S 23825pt, R, May 1987, damaged distally but more or less intact. GRAVEYARD 1, NMNZ, S 23664pt, ?, shaft, larger than L? with same number. GRAVEYARD 3, NMNZ, S 23825pt, R, May 1987, proximal end missing, distal end damaged. HIS & HER, NMNZ, S 23435, L, T H Worthy,. NMNZ, S 23439, L, T H W, distal, very badly eroded-eaten?. NMNZ, S 23434, R, T H Worthy, slight wear. NMNZ, S 23436, R, broken, restored, worn proximally and distally, noted as left on loose sheets. NMNZ, S 23437, R, T H Worthy, olecranon worn, damaged distally. NMNZ, S 23438, R, T H Worthy, worn proximally and distally. MT OWEN, SO 209, NMNZ, S 27773, L, Jan 1990, R, Jan 1990, part of complete skeleton, distal cranial section of R broken. OAMARU, AU, AU9723, R, P R Millener J A Grant-Mackie, broken near proximal end, portion missing but junction still present. SHIRLEY CREEK, NOM, Bruce McCulloch, 1979, per Bruce McCulloch.

6.5.8.17 *RADIUS*

Haast (1874: 71, description; pl. VIII 5, 6): "The proximal end is well expanded, and the tubercle for the insertion of the biceps stands considerably forward, the shaft becoming afterwards very flat towards the ulna, not being so much bent as in *Aquila.*

"The radius of *Harpagornis assimilis* ... is, like the ulna, of much stouter proportions. It is more bent towards it distal extremity, so that the same stands at a greater angle to the shaft than any of the recent species."

Owen (1879: 145; pl. CVI 4): "The radius is thicker in proportion to its length, and also in proportion to the ulna, in *Harpagornis,* than in existing Raptores. The ridges and processes indicative of the power of the muscles of flight are strongly marked, especially the tubercle near the proximal end for the

insertion of the main tendon of the biceps. The shaft is more bent toward the distal end, as Von Haast has observed, than in existing birds of prey."

Description. (Plate 12, fig. C-D; Table 6.10).

Material available. CASTLE ROCKS, OM, C 40.8, L, R, A Hamilton, 1893. NMNZ, DM 2134pt, R, A Hamilton, 1891/2, "on the surface (in the fissure) at the extreme end of the cave, under the overhanging rock", perfect condition for illustration. ENFIELD, CM, AV 5329pt, R, P H & H O Forbes. ENFIELD?, BMNH, 14, L, H O Forbes?. BMNH, none, R, H O Forbes?. OAMARU = ENFIELD, BMNH, A 423 pt, L, H O Forbes, presented 1894. GLENMARK/WEST, CM, AV 5104pt, L, R, Haast party, 1873, fragments. HAMILTON, AIM, 574pt, B S Booth? F W Hutton. EAGLE ROOST H, NMNZ, S 22472.4, ?, P R Millener, 26 Oct 1982, distal end eroded. NMNZ, S 22472.5, ?, P R Millener, 26 Oct 1982, proximal end eroded. GRAVEYARD 3, NMNZ, S 23825pt, ?, May 1987, broken, repaired. GRAVEYARD lag, NMNZ, S 23073.2, R, T H Worthy, broken in 2 places, repaired. GRAVEYARD/terrace, NMNZ, S 23051.5, L, proximal L?. NMNZ, S 23051.4, R, proximal R?. HIS & HER, NMNZ, S 23445, ?, T H Worthy, 3 fragments. NMNZ, S 23443, L, T H Worthy, prox?. NMNZ, S 23440, R, T H Worthy. NMNZ, S 23441, R, T H Worthy. NMNZ, S 23442, R, T H Worthy, dist?. NMNZ, S 23444, R, T H Worthy, dist?. MT OWEN, NMNZ, S 27773, L, R, Jan 1990, part of complete skeleton. NGAPARA, OM, C 03.61pt, L, A Hamilton 1903, proximal. OARO, CM, AV 5333pt, R, O B Stanford 1937. OLD RIFLE BUTTS, CM, AV 24887pt, L, R J Scarlett, 1-2 Sep 1970, prox?. CM, AV 24887pt, R, R J Scarlett, 1-2 Sep 1970, part. SHIRLEY CREEK, NOM, Bruce McCulloch 1979, per Bruce McCulloch.

6.5.8.18 *CARPOMETACARPUS*

Haast (1874: 71; pl. VIII 7): "It is only a little longer than that of *Aquila,* but also much stouter in its proportions. This is most conspicuous in the medius metacarpal and the proximal end.

"The process for the attachment of the index phalanx is broad and heart-shaped, and the two principal intermuscular ridges upon the medius metacarpal enclose a broad and well-defined channel."

Owen (1879: 146) quotes Haast's description.

Scarlett (1972: fig. 118).

Description. (Plate 12, fig. E-F; Table 6.11). Pisiform process large, square-ended. Anterior carpal fossa shallow; small foramina in internal ligamental fossa. At proximal end, line between apices of internal and external carpal trochleae only slightly concave. Pollical facet notched proximally and distally, dividing surface into two segments. Tendinal groove distinct, bifurcating about 25% of length from distal symphysis. Posterior carpal fossa distinct, rectangular, reaching almost to base of metacarpal III.

Material available. CASTLE ROCKS, NMNZ, DM 2134pt, L, complete, R, lacking most of minor metacarpal, A Hamilton, 1892. OM, C 40.8pt, L, missing most of minor metacarpal, R, A Hamilton, 1893. ENFIELD?, BMNH, 35, L, Forbes?. BMNH, 36, R, Forbes?. BMNH, R3184, ?, Collection of H O Forbes, 1891 or 1892. GLENMARK/EAST, CM, AV 5102pt, L, Haast party, 1873, part of *Harpagornis assimilis* type series. HAMILTON, AIM, 574pt, B S Booth? Hutton. HAMILTON OR ENFIELD, CM, AV 6291, L,. GRAVEYARD, NMNZ, S23664pt, L, major metacarpal. NMNZ, S 22653pt, R, P R Millener, 4 Apr 1983. AR 144, NMNZ, S 23611pt, L. EAGLE ROOST H, NMNZ, S 22472.7, L, P R Millener, 26 Oct 1982, lacking most of minor metacarpal. NMNZ, S22472.8, R, P R Millener, 26 Oct 1982, perfect. GRAVEYARD 3, NMNZ, S 23825pt, L, May 1987. HIS & HER, NMNZ, S 23454, L, T H Worthy, proximal only. NMNZ, S23455, L, T H Worthy, major metacarpus + proximal. NMNZ, S 23456, R, T H Worthy. NMNZ, S 23457, R, T H Worthy, major metacarpal. NMNZ, S 23458, R, T H Worthy, major metacarpal shaft + prox. HIVES EXTENSION, NMNZ, S 25582, L. KING'S CAVE, CM, AV 22481, R, G Wilson & Canterbury Caving Club, 29 Sep 1968, dist fragment. MARFELLS BEACH, CM, AV 11163, L, J R Eyles, Apr 1952, proximal anterior section missing. MOTUNAU, NMNZ, DM 2143pt, L, A McKay, 1881 or 1882, part only. MT OWEN, NMNZ, S 27773, L, R, D Smith T H Worthy P R Millener, Jan 1990, parts of complete skeleton. NGAPARA, OMNZ, C 32.81, L, A G Gilkison, 1932, proximal end plus major metacarpus.

6.5.8.19 *ULNARE*

Description. (Plate 12, fig. G-H).

Material available. AR 144, NMNZ, S 23611pt, ?. GRAVEYARD, NMNZ, S 23051.3, L, JD, P R Millener. MT OWEN (SO 209), NMNZ, S 27773pt, L, R, D Smith T H Worthy P R Millener, Jan 1990, part of complete skeleton.

6.5.8.20 *RADIALE*

Description. (Plate 12, fig. I-J).

Material available. CASTLE ROCKS, NMNZ, DM2134pt, ?, A Hamilton. NMNZ, S 27773pt, L, R, D Smith T H Worthy P R Millener, Jan 1990, part of complete skeleton.

6.5.8.21 *POLLEX, MAJOR DIGIT PHALANGES, MINOR DIGIT PHALANX*

Description. (Plate 12, fig. K-O).

Material available. CASTLE ROCKS, NMNZ, DM 2134pt, ?, A Hamilton. OMNZ, C 40.8pt, R, A Hamilton 1893. AR 144 L2, NMNZ, S 23611pt, ?. GRAVEYARD, NMNZ, S 23073.3, ?. MT OWEN (SO 209), NMNZ, S 27773pt, L pollex, major 1, minor 1, R pollex, major 1 and 2, minor 1. WAINGONGORO, BMNH, 32245h, L major 1, W Mantell 1847?, purchased BMNH c1855.

6.5.8.22 *FEMUR*

(Haast 1872: 193-194, pl. X, fig. 1, 4, 5; original description): "The principal bone in the collection is a left femur [from] a mature bird, as shown by the excellent

preservation of the articular extremities and the strongly developed muscular ridges. (Plate X, fig. 1, 4, 5)

Total length	6.66 inches [169.2 mm]
Proximal circumference	4.66 inches [118.4 mm]
Distal circumference	5.58 inches [141.7 mm]
Least shaft circumference	2.50 inches [63.5 mm]

"This bone has all the characteristics of the femur of a diurnal bird of prey, some of them developed in a remarkable degree owing to its enormous size. The cylindrical shaft is bent forward as usual, and above the distal extremity it is slightly curved back. I find that both the *Polioaetus* [=*Haliaeetus leucogaster*] and *Circus* possess this curve, but the latter exhibits this peculiarity much more distinctly than the Australian species. The hollow on the top of the head is very large, and measures .42 inch [10.7 mm] across. The trochanteric ridge is well developed, and the outer side is very rough, showing that muscles of great strength and thickness must have been attached to it. The inter-muscular ridges are well raised above the shaft, of which the one extending from the fore and outer angle of the epitrochanteric articular surface to the outer condyle is the most prominent. The pits for the attachment of the ligaments in the inter-condylar fossa are strongly marked. The femur is pneumatic, the proximal orifice is large and ear-shaped, resembling in form more the air passage of the New Zealand *Circus* than that of the Australian Sea Eagle, the only two bones I possessed for comparison. The junction of the bend with the shaft is more deeply cut and more distinctly defined than in *Polioaetus*, the same being the case with *Circus,* so that the trochanter of both are more rounded and distinct than in the Australian Eagle. The angular concavity on the [distal surface of] the outer condyle is of considerable size and depth. Also in this point the close resemblance of the fossil bone to the corresponding limb bone of our present Harrier is very striking.

Haast (1874: 65, measurements; 65-66, description): "[In comparison with *Aquila audax*] This bone, besides being of smaller dimensions, is somewhat slighter in its form, otherwise the description as given of that of *Harpagornis moorei* closely corresponds in all its principal points. There is no doubt, judging

from the insertion marks of the muscles and the intermuscular linear ridges, that this species was also very powerful. Of the latter the linea aspera is not quite continuous, being repeatedly interrupted at more or less considerable intervals. The form of the proximal orifice is somewhat different from that of *H. moorei*, it being more rounded; however, this may be a sexual or even individual peculiarity, and of no specific value.

"Examining the femora of a male and a female *Circus,* I observe that this proximal orifice in the larger female is also oval, and in the smaller male more rounded off."

Owen (1879: 146-147; pl. CVII 1, 2, 3, 4): "With the usual characteristics of this bone in the Raptorial order, the femur of *Harpagornis* is remarkable for its greater relative thickness and the greater expanse of its extremities, especially of the distal one. The pneumatic foramen is large, single, and situated, as usual in the Order, on the fore part of the bone between the praetrochanterian ridge and the supporting base of the head of the femur; no constriction, like a 'neck' is present; and the head, from which the articular cartilage was extended along the upper surface of the supporting base to the great trochanter, is as characteristically sessile as in other Raptores. The ectotrochanterian ridge is less convex in contour than in the Golden Eagle (*Aquila chrysaetos*); the hypotrochanterian roughness for the insertion of the intrapelvic muscle, which I have called 'obdurator internus' in the Apteryx, has more the form of a ridge in *Harpagornis* than of a tubercle.

"The praetrochanterian ridge is linear, and may be traced down the middle of the fore part of the shaft; its continuation into the antentocondylar ridge is interrupted. This ridge, as well as the antectocondylar ridge, is well marked, and relatively sharper than in *Aquila.* The rotular channel is broad and deep. The popliteal space is shallow. The distal end of the femur is relatively broader transversely than in *Aquila.* The intercondylar ridge is well marked. The backward production of the inner condyle dividing the tibial facet from the fibular facet is relatively more produced and sharper. Every character of the femur indicative of muscular force and strength of joint is better marked than in the smaller existing Raptorial birds, although inferior, especially as regards the

posterior ridges of the shaft, or 'linae asperae,' to that bone in the huge objects of prey of the *Harpagornis.* The least circumference of the femoral shaft in the larger (female?) *Harpagornis* is 2 inches 6 lines, in the smaller (male?) specimen 2 inches 3 lines)."

Oliver (1955: 604): "Shaft bent forwards; hollow on top of head large; trochanteric ridge well developed, roughened; inter muscular linear ridges raised; proximal pneumatic orifice large and ear-shaped."

Scarlett (1972: fig. 194).

Description. (Plate 1, fig. A-F, lectotype; Plate 2, fig. A-D, lectotype femur *H. assimilis*; fig. E-F; Plate 13, fig. A-D; Table 6.12). Head round in proximal view. Impression of round ligament deep, to proximal side. Distinct neck; iliac facet demarcated by low ridge. Trochanteric ridge low, rounded; cranial surface (including foramen) smoothly, shallowly concave; small foramina along distal to edge of iliac facet and around to just under slight overhang of head. Pneumatic foramen <0.5x length of trochanter. Intermuscular line passes closely medial to foramen, becoming obscure at 33%-50% length of shaft. Epicondylus medius flattened. Rotular groove narrow. Fovea tendineus M tibialis triangular, apex craniad. Fibular groove broad; lateral epicondyle large, with prominent fossa proximally. Popliteal fossa shallow, with foramina. Fossa trochanteris almost obsolete. Foramina along caudal edge of head, iliac facet, and the low obdurator ridge.

Material available. NO LOCALITY, NMNZ, DM 2138, L, {518} CAST. NMNZ, DM 2145pt, R. CASTLE ROCKS, OM, C 40.8pt, L, R, A Hamilton, 1893. ENFIELD?, BMNH, 10, L, ?Forbes, head and trochanter worn, condyles worn. BMNH, 11, R, Forbes?, worn on trochanteric surface, and on internal condyle. GLENMARK/WEST, CM, AV 5104pt, L, F R Fuller, 1871, designated LECTOTYPE (Holdaway 1990). GLENMARK/EAST, CM, AV 5102pt, L, R, J Haast party, Jul-Aug 1873, part of *H. assimilis* type series. HAMILTON SWAMP, OMNZ, unnumbered, L, F W Hutton B S Booth, 1873?, with Hutton label, trochanter damaged. HAMILTON GULLY, AIM, 574pt, B S Booth?, distal only. AR 144, NMNZ, S 23611pt, R. EAGLE ROOST H, NMNZ, S 22472.9, L, P R Millener, excellent condition. NMNZ, S 22472.10, R, P R Millener, excellent condition. GRAVEYARD 3, NMNZ, S 23030pt, L, calcite encrustation proximally and distally. NMNZ, S 23825pt, R, May 1987, missing lateral condyle. NMNZ, S 23825pt, R, May 1987. HIS & HER, NMNZ, S 23462, L, abraded proximally and distally. NMNZ, S 23464, L, worn proximally and distally, gnawed by rats. NMNZ, S 23465, L, in 2 pieces. NMNZ, S 23463, R, badly abraded proximally and distally. MARFELLS BEACH, CM, AV 9651, R, R S Duff, 5 Oct 1944, proximal part missing (most). MOTUNAU, NMNZ, DM 2143pt, R, A McKay, 1882. MT OWEN, NMNZ, S 27773, L, R, D Smith T H Worthy P R Millener, Jan 1990, parts of a complete skeleton, right worn distally. OAMARU/WANBROW, AU, AU 9723, L, R, P R Millener J A Grant-Mackie,

both cleanly broken and mended. OLD RIFLE BUTTS, CM, AV 24887pt, L, R J Scarlett, 1-2 Sep 1970, damaged, distal part only. PYRAMID VALLEY, Sq 60, CM, AV 28366, L, J R Eyles R J Scarlett, 16 Feb 1949.

6.5.8.23 *TIBIOTARSUS*

Haast (1874: 66, measurements; 66-67, description, pl. VII 1, 2): "The same pachydermal character, ... distinguishes ... this bone, ... from any bird of prey known to inhabit New Zealand at present.

"Even in comparing the same with that of *Aquila audax,* ... with which it has otherwise many features in common, this character is well exhibited.

"The from of the surface of the proximal end agrees well in both species, with the exception that the proximal [note in Hutton's handwriting in his copy 'procnemial'] ridge is more rounded off, and the intercondylar tuberosity stands higher in *Harpagornis,* in which two features the fossil bone agrees more with *Circus.*

"Two narrow and low intermuscular ridges are well marked, the first of which begins at the base of the procnemial process and extends to the inner side of the extensor tendinal canal, above the bony bridge spanning over the precondylar groove; the other at the termination of the vertical fibular ridge, descending the shaft in a transverse line till it has crossed two-thirds of its breadth, within one inch above the bridge, then retreating again with a gentle curve. After forming the outer boundary of the groove, it then terminates on the outer side of the canal for the extensor tendon; thus differing from *Aquila,* where this second ridge reaches only to the middle of the shaft, and does not describe such a considerable arc as we observe upon the fossil bone.

"The distal condyles are well curved at their anterior ends, and have a more rounded form (which the outer shows most conspicuously than either *Aquila* or *Circus,* in which they are more oblong. Moreover, those of the recent species stand more in advance of the shaft.

"The inner distal condyle is also more developed in a transverse extent than the outer one - a feature also exhibited by *Aquila.*

"The shaft of the bone, although slightly bent backwards near its proximal end, is, however, straighter than in *Aquila,* but not so straight as that of *Circus.* The fibular ridge is strongly developed."

Owen (1879: 147; pl. CVII 5, 6): "This bone in *Harpagornis* corresponds with the femur in its strength, i.e. in the proportions of breadth to length of shaft.

"The procnemial ridge is more pronounced at its upper part than in the Eagles, but sooner subsides into the lower less prominent ridge which is continued down the fore part of the shaft, inclining towards the innermost of the distal condyles. The depression on each side of the procnemial ridge is well marked; the inner (tibial) one is bounded by the low, thick, obtuse 'entocnemial' ridge, extending from the overhanging (tibial) border of the proximal articular facet of that side of the head, obliquely downward and forward to join or be lost in the procnemial ridge. The outer depression has the form of a wide vertical channel, and is bounded externally (fibulad) by the ectocnemial process. The fibular ridge is well marked; it is relatively more prominent, but is minor longitudinal extent, than in the Eagles. The ectarticular convexity is smoothly rounded; the rugous facet anterior to it for the 'crucial' ligament, and that attached to the head of the fibula, are well marked. The two distal condyles show a breadth which exceeds by two fifths that of the same part of the leg-bone in the Condor or Lammergeyer. In their proportions, shape, and degree of anterior convexity these condyles exhibit the Falconine characters of this end of the tibia. The praecondylar groove is crossed by the osseous bridge, as in the 'Diurnal' division of Raptores. The strength of the 'tibialis anticus' muscle is significantly indicated by the size of the bony canal which was traversed by its tendon."

Scarlett (1972: fig. 195).

Description. (Plate 14, fig. C, D; Table 6.13) Popliteal crest high, broad. Medial cnemial crest curved for proximal 50%, then notched by groove from median surface, then parallel with shaft. Ligamental attachment short. Medullary artery foramen just distal to distal end of fibular crest. Fibular crest to >33% length of shaft. Fibular spine ends c16% shaft length from distal end.

Supratendinal bridge narrowing abruptly distally. Intercondylar fossa <33% distal width, with proximal and distal lateral fossae and central ridge.

Material examined. NÖ LOCALITY, NMNZ, DM 2146pt, L, shaft only. NMNZ, DM2145pt, R, dist [71]. ALBURY PARK, CM, none, R, B McCulloch, on display, not measured, collection of B McCulloch. CASTLE ROCKS, OM, C 40.8 pt, L, R, A Hamilton, 1893. NMNZ, DM 2134pt, R, A Hamilton. ENFIELD?, BMNH, 16, L, ?Forbes, length without crest 229.2. BMNH, 15, R, Forbes?, varnished, large nutrient foramen lateral, c 5mm from distal end of fibular crest. GLENMARK/EAST, CM, AV 5102pt, L, R, both part of *Harpagornis assimilis* type series, Haast party, 1873. GLENMARK/WEST, CM, AV 5104pt, L, R, Haast party, 1873, not part of type series. HAMILTON SWAMP, BMNH, A 2119, L, "*Harpagornis assimilis,*" Forbes collection, transferred from Zool Dept 1934, proximal end only. CM, AV 5324pt, R, B S Booth, Jan 1874, worn proximally. AR 144, NMNZ, S 23611pt, R. EAGLE ROOST G, NMNZ, S 22473.6, R, P R Millener, 25 Apr 1983. NMNZ, S22473.7, R, P R Millener, 25 Apr 1983. EAGLE ROOST H, NMNZ, S 22472.11, L, P R Millener, 26 Oct 1983, perfect. GRAVEYARD, NMNZ, S 22653pt, L, 4 Apr 1983. GRAVEYARD 3, NMNZ, S 23825pt, L, May 1987, distal end + shaft. HIS & HER, NMNZ, S 23467, L, T H Worthy, worn proximally and distally. NMNZ, S 23470, L, T H Worthy, broken, repaired, worn proximally and distally. NMNZ, S 23466, R, T H Worthy, 2 joinable pieces + fragments. NMNZ, S 23468, R, T H Worthy, 3 pieces, joined, part proximal end missing through wear, distal end worn. NMNZ, S 23469, R, T H Worthy, worn proximally, abraded distally. NMNZ, S 23471, R, T H Worthy, shaft only. KAPUA SWAMP, CM, AV 5322, R, F W Hutton, ZFS 686.5, proximal end damaged. MARFELLS BEACH, CM, AV 11041, L, J R Eyles, Apr 1952, part shaft + distal end. MOTUNAU, NMNZ, DM 2143pt, L, A McKay, 1882, dist. MT OWEN, NMNZ, S 27773, L, R, D Smith T H Worthy P R Millener, Jan 1990, part of complete skeleton, slight proximal and distal wear on R. OARO, CM, AV 5333pt, L, O B Stanford, 1937, previously on display, located 11 Apr 1988 with *Aptornis* skeleton. SHIRLEY CREEK/WANBROW, NOM, Bruce McCulloch, 1979, per Bruce McCulloch. TE AUTE, NMNZ, DM 2144, R, A Hamilton, distal end + shaft. WAKAPATU?, OM, C32.66pt, D Teviotdale 1932?, not found 24 VII 87. OM, C32.66pt, D Teviotdale 1932?, not found 24 Jul 87.

6.5.8.24 *FIBULA*

Haast (1874: 67-68; pl. VII 3, 4): "Amongst the smaller bones obtained from the locality where the principal portion of the skeleton of *Harpagornis moorei* was excavated are a pair of fibulae, which, on closer inspection, proved to belong to that skeleton. Of these the right one is the most perfect. It is 4.27 inches long, the distal point being broken off.

"The articular head, 0.80 inch long and 0.31 inch broad, is very large and posteriorly slightly convex, its anterior edge sloping down at a considerable angle, far more than in *Aquila* or *Circus,* in which the articulating surface is nearly plane, and stands at a right angle to the shaft. The head is also far more hollowed out on the inner side than *Aquila.*

The shaft in its upper portion is considerably bent backwards, and very broad where it is attached to the tibia, after which it decreases rapidly in size. Two shallow pits for the insertions of tendons are well marked."

Material examined. CASTLE ROCKS, OMNZ, C 40.8, R, A Hamilton, 1893. ENFIELD?, BMNH, 17, L. BMNH, 18, R, Forbes, 1892. GLENMARK/WEST, CM, AV 5104pt, L, CM party. CM, AV 5104pt, R, CM party. EAGLE ROOST H, NMNZ, S 22472.12, L, includes spine. NMNZ, S 22472.13, R, includes spine. GRAVEYARD 1 L3, NMNZ, S 23664pt, ?. HIS & HER, NMNZ, S 23476pt, L. NMNZ, S 23476pt, R, MT OWEN, NMNZ, S 27773pt, L, R, tomo SO209, with spines, parts of complete skeleton.

6.5.8.25 *TARSOMETATARSUS*

Haast (1874: 68, measurements; 68-69, description; pl. VII, 5, 6): "In its general form also, this bone resembles in its main features that of *Aquila,* except being somewhat more robust.

"The shaft at its upper end is expanded and transversely flat, gradually becoming narrower, and assuming towards its middle a trihedral shape, after which it flattens again above the fore and aft canal, between the middle and outer metatarsal, near their distal ends.

"In *Circus* the trihedral portion of the bone is much longer, even in comparison to its whole length, than either in the fossil bone or in *Aquila.*

"The form and position of the trochlear condyles agree more closely with *Circus,* they being broader and with a larger space between them than in *Aquila.*

"The tuberosity for the insertion of tibialis anticus is remarkably developed, another proof of the great power the fossil bird must have possessed.

"The ectocondylar concavity is well marked, far more than in the recent species, in both of which the outer side of the proximal surface is almost plane.

"The three tendinal grooves between the calcaneal processes and the inner posterior ridge are deeply excavated, much more than in *Aquila audax.* Half-way down the shaft they unite to form one concave channel, which, above and close to the process for the attachment of the metatarsal of the back toe, runs out to a flat surface.

"The two fore and aft foramina in the upper part of the bone, in the grooves near the base of the anterior intercondylar prominences, are well marked.

"The surface of the bone running from the outer margin of the ectocondylar ridge down to the outer condyle is very broad and flat, as in *Aquila,* having its greatest diameter in the middle portion of the bone, thus forming the base of its trihedral form.

"In *Circus* the base of the bone is situated more in its posterior portion, the ridge running towards the centre of the anterior portion of the shaft, giving the latter a triangular form for about two-thirds of its entire length.

"[Bone attributed to *H. assimilis*] The shaft of this bone, if we compare its total length with that of *H. moorei*, is generally narrower; this is most conspicuous above the deeply excavated process for the attachment of the back-toe metatarsal, where the shaft is thinnest.

"The ectocondylar ridge is also more pronounced, by which the shaft assumes a more triangular form than it possesses in the larger species. The two posterior ridges on both sides of the concave channel are more sharply defined, so that the latter is deeper than in *H. moorei*, approaching in form more that of [*Aquila audax*]."

Owen (1879: 147-148; pl. CVI [not CVII as on p. 147] 5, 6): "In the metatarsus of *Harpagornis* the indications of the power of the raptorial foot reach their maximum. This will be evident to any one comparing the ... figures with those of the metatarsus of the Golden Eagle (*Aquila chrysaetos*). From that type the present fossil differs in its greater breadth and thickness in proportion to its length, and especially in the greater strength and outward extension of the condyle for the innermost of the anteriorly directed toes; the shaft of this composite bone is rather more twisted on its axis, with a greater inclination of the stem of the condyle backward. The 'entocondylar cavity' is somewhat deeper and larger than the ectocondylar one; the intercondylar tubercle is large, but little elevated. The ectocalcaneal process is a strong and prominent subquadrate of bone. The entocalcaneal process is, as usual in Raptores, of smaller size. The intervening calcaneal groove or channel is of great depth and width. Into the

wide and deep antinterosseal depression open the entinterosseous and ectinterosseous canals. The small hinder orifice of the latter remnant of the primitive interspace between the ecto- and mesotarsal elements is shown in fig. 6, at m. The ectinterosseous groove is continued down a short way below this orifice. A strong tuberosity marks the insertion of the tendon of the 'tibialis anticus'. The entogastrocnemial ridge is continued from the entocalcaneal process nearly half way down the shaft of the metatarsus. The ectogastrocnemial ridge and the postinterosseous ridge are well developed. The intermuscular ridges on the fore part of the shaft are equally well marked; the entometatarsal ridge is shown at q, the ectometatarsal ridge at k. A long groove for the 'adductor digiti externi' deepens as it leads to the foramen, through which the tendon of that small muscle glided to the interspace between the meso- and ectotrochleae. A strong osseous bridge divides the upper and hinder orifice from the intertrochlear outlet of the tendinal canal. The depth and extent of the surface for the ligamentous attachment of the innermost and backwardly directed metatarsal bespeak of the strength of the toe opposing the forwardly directed digits in the grasping actions. The ectotrochlea is, transversely, rather narrower than usual relatively to the other trochleae; but it is of equal antero-posterior extent. The least circumference of the shaft of the metatarsal of *Harpagornis moorei* is 2 inches; the breadth of the two extremities and the length of the bone are shown in PL. CVI."

Scarlett (1972: fig. 196).

Description. (Plate 13, fig. E-F; Plate 14, fig. A, B; Table 6.14) Anterior proximal fossa (fossa infracotylaris dorsalis more deeply excavated than in *Aquila*. Scars of anterior vinculum (Impressiones retinaculi extensorii) proportionately closer, and on same level: lateral higher than medial in *Aquila*. Cranial edge of proximal internal cotylar surface overhangs cranial fossa (not in *Aquila*): lateral articular surface extends further cranio-distally in *Harpagornis*. Lateral cotyla extends further proximally than medially. Lateral notch for peronaeus nerve more formed (complete) laterally than in *Aquila*: definite rectangular tab arising from proximal lateral margin. Lateral hypotarsal crest rectangular in caudal view; triangular in *Aquila*. Medial crest c25% of tarsometatarsus width laterally; less

in *Aquila*. Medial hypotarsal ridge long proximo-distally as in *Aquila*, not short as in *Aegypius*. In *Aegypius* and *Gyps* hypotarsal ridges combined, occupying much of plantar surface of shaft proximally. Facies subcutanea lateralis extends further laterally in *Harpagornis* than in *Aquila*. Condyle IV, lateral flange flaring laterally, not incurved as in *Aquila*. Transverse section at mid-point of shaft ± triangular. Sulcus flexorius shallow. Lateral foramen vascularis proximale on median side of lateral edge of shallow fossa distal to lateral hypotarsal crest, as in *Aquila*. Median foramen medial to distal end of median crest. Furrow lateral to insertion of tibialis anticus not as deep as in *Aquila*, surface of bone running ± smoothly to lateral margin; definite furrow in *Aquila*. Trochlea III with raised cranial edge, 'obtusely' rounded in outline. Cranio-medial edge of trochlea III notched as in *Aquila*. In trochlea IV, outline of process truncated to rounded in lateral view, not produced as in *Aquila*. Lateral fovea of trochlea deep, straight-edged cranially. Trochlea is as in *Aquila*, except that cranial edge more clearly defined as step. Fossa metatarsi I plantar medial, breaking outline of crista plantaris media. Inner cotyla much larger, anterior edge almost straight, medial edge at 90°. Intercotylar area with low relief; prominence low; anterior edge prominently notched lateral to prominence. Anterior lip faces extending equally down anterior face. Fossa infracotylaris dorsalis broad and deep; with foramina near distal end; medial foramen slightly more distal. Impressiones retinaculi extensorii visible on AV 5104; lateral impression proximal to median, under cotylar lip and on wall of fossa; medial impression 0.5x way between lateral impression and medial margin, on inner face of metatarsal ridge. Tibialis anticus impression prominent, about twice as long proximo-distally as broad; c25% shaft length from proximal end. On caudal surface, medial foramen piercing medial to and against base of medial calcaneal ridge; groove continuing distally from foramen. Lateral foramen pierces bone in centre or slightly medial to centre of lateral crest, right at base of main crest. Medial ridge twice as high as lateral, turned over medially at proximal and plantar (caudal) edges. Lateral ridge square and blocky at base, then turning c45° laterally to form posterior part of N. peronaeus notch. Small flange (extension of lateral margin) arising at proximal end to form remainder of semicircular notch. Laterally deflected part

of lateral ridge 50% proximal distance of length of median ridge. Mid-shaft subtriangular in section, slightly concave on plantar (caudal) surface = shallow sulcus flexorius, but lateral flange not developed. Antero-lateral surface planar to slightly concave; antero-medial surface concave. Medial anterior surface "turned" antero-posteriorly. Fossa metatarsi I twice as long proximo-distally as wide; at c30° to posterior margin. Medial edge projecting past median margin, visible in cranial view. Attachment of external ligament a broad pit. Trochlea III large, central groove narrow, deep, c33% of trochlea width. Trochlea II wing square-ended in cranial view, ending in proximal and distal tubercles best seen in medial view. Trochlea II width = width trochlea IV. Distal foramen large, extensor groove extending to level of proximal end of metacarpal facet. Flexor groove for digit II notching medial margin of shaft. Fovea ligamentum collateralis oval, with well-developed proximal border.

Material examined. NO LOCALITY, NMNZ, DM 2139, R, dune material? from appearance. CASTLE ROCKS, NMNZ, DM 2134pt, L, A Hamilton, 1892/3. CASTLE ROCKS, OM, C 40.8pt, L, R, A Hamilton, 1893. DUNSTAN RANGE, NMNZ, DM 2136, R, A Hamilton. ENFIELD SWAMP, CM, AV 5329pt (Fig. 6.4), R, P H & H O Forbes. ENFIELD?, BMNH, 19, L, Forbes?. BMNH, R, Forbes?, ext edge peronaeus notch worn. GLENMARK/EAST, CM, AV 5102pt, L, R, Haast party, 1873, part of *H. assimilis* type series. GLENMARK/WEST, CM, CM 5104pt, L, R, Haast party, 1873, not in type series. HAMILTON SWAMP, CM, AV 5324pt, R, B S Booth, Jan 1874. HIVES EXTENSION, CM, AV 36397, R, M M Trotter, P Wood, 23-26 Oct 1981, worn proximally. EAGLE ROOST G, NMNZ, S 22473.8, R. EAGLE ROOST H, NMNZ, S 22472.14, L, P R Millener, 25 Apr 1983, ± perfect. GRAVEYARD, NMNZ, S 23664pt, R, dist. NMNZ, S 23073.1, R, T H Worthy. GRAVEYARD 1, NMNZ, S 23720pt, L, shaft. GRAVEYARD 3, NMNZ, S 23825pt, L, May 1987, dist missing exc condyle digit IV. NMNZ, S 23825pt, R, May 1987, in matrix. NMNZ, S 23825pt, L, May 1987, prox broken, ext condyle missing, broken, repaired. HIS & HER, NMNZ, S 23473, L, worn prox, broken, repaired. NMNZ, S 23474, L. NMNZ, S 23475, L, prox badly eroded, intercotylar area OK. NMNZ, S 23472, R, broken, repaired. NMNZ, S2 3477, R, prox. KAKANUI BEACH, CM, AV 29361pt, L, washed from bank by high tides, J Park per Cyril {illegible}, worn, Oct 1974. MARFELLS BEACH, CM, AV 12263 (Fig. 6.4), L, J R Eyles, 1947, Te Hau (property of D Dick), CM, AV 16221, L, Ruby Britton, Jan 1959, prox missing. MOTUNAU, BMNH, 93.1.30.21/, R, H O Forbes, part of A 1512. NMNZ, DM 2143pt, R, A McKay, 1882. MT OWEN (SO 209), NMNZ, S 27773, L, R, D Smith T H Worthy P R Millener, Jan 1990, part of complete skeleton. NGAPARA, OMNZ, C 32.83pt, L, A G Gilkison, 1932, brittle, intact. OM, C 03.60, R, A Hamilton, 1903. OMNZ, C 32.83pt, R, A G Gilkison, 1932, shaft only, brittle. SHIRLEY CREEK/WANBROW, NOM, Bruce McCulloch, 1979, per Bruce McCulloch. NOM, Bruce McCulloch, 1979, per Bruce McCulloch. WAKAPATU? OR NGAPARA?, OM, C 32.67pt, D Teviotdale, 1932?, not found 24 VII 1987. OM, C 32.67pt, D Teviotdale, 1932-?, not found 24 VII 1987. WARRINGTON, NMNZ, DM 2137, L, A Hamilton.

6.5.8.26 *PEDAL PHALANGES & FIRST METATARSAL*

(Haast 1872: 195; pl. XI 1): "Two ungual phalanges, of which the largest one (Pl. XI., figs. 1 and 1a), measures as follows:

Length from summit of articular end to point, 2.92 inches [74.2 mm]

Circumference near articular end, including lower process, 3.17 inches [80.5 mm]

As far as the scant material for comparison will allow, I believe that this bone is the ungual phalanx of the hallux or first toe of the left foot. A comparison with fig. 3, Pl. XI., the ungual phalanx of the left foot (hallux) of the *Aquila audax*, the great Wedge-tailed Eagle of Australia, and with fig. 4, the corresponding bone in the New Zealand Harrier, will not only prove the close resemblance between that bone, belonging to these birds and the *Harpagornis,* but also their striking difference in size.

"A second ungual phalanx, applying the mode of measurement previously used, is 2.75 inches [69.9 mm] long, and has a circumference of 2.92 inches [74.2 mm]. It belongs probably to the second toe of the right foot. Pl XI., fig, 2, shows its articular proximal surface."

Haast (1874: 75): "Since my former [i.e. 1872] paper a second ungual phalanx has been obtained, which, applying the same mode of measurement previously used, is 2.75 inches long, and has a circumference of 2.92 inches at its proximal end. It is the third phalanx, and belongs to the second or inner toe of the right foot.

"Amongst the smaller bones lately excavated I found also the second phalanx, with which that latter ungual phalanx articulates.

"The pachydermal character, even in these toe-bones is well sustained, and the form and peculiarities of the articular ends, and the large concavity behind and below the trochlear joints of the distal end, are developed in a striking degree."

Owen (1879: 148-149; pl. CVII 7): "Assuming this ungual phalanx to correspond with the one which is commonly the largest in diurnal raptores, viz. that which supports the back toe (digit i), a second somewhat smaller claw-bone, discovered at the same time and place, and differing only in a slight inferiority

of size, may well be a claw-bone of the toe iii. Subsequently a third ungual phalanx was discovered in another part of the Glenmark swamp, of rather less length than the second, but of equal size of basal articulation, and with it the penultimate phalanx of the same toe. On the assumption that the largest claw-bone was that of the 'hallux', or hind toe (i), it may be compared with the homologous bone in ... [*Aquila audax*]... and with that in [*Circus approximans*]. In all diurnal Raptores such ungual phalanx is characterized not only by its size, but by its curvature, its gradual tapering to a sharp point, by the depth of the pair of trochlear cavities at its base fitting closely or interlocking with the distal condyles of the penultimate phalanx, and above all by the size and prominence of the lever for the insertion of the flexor tendon of the claw phalanx, which recalls the corresponding element in the retractile claw-bones of the Tiger. The process in question, in its direction and extent, resembles that in the Falcons and Harriers more than that in [*Aquila audax*] or in the Eagles."

Scarlett (1972: fig. 197).

Description. (Plate 15, fig. A-O; Fig. 6.3). Typical of large accipitrids, but much more robust. Phalanges of digits one and two extremely robust, almost twice as broad as those of digits three and four. Flexor process of ungual phalanges deep, claw deep at base; ungual phalanges of digites one and two twice as long as those of three and four. Proximal phalanges of digit two not fused, but joint probably immobile in life.

Material available. NO LOCALITY, CM, AV 10472, "Before 1950". CASTLE ROCKS, OM, C 40.8, x phalanges, 1 metatarsal, including x elements from DM 2134 individual, A Hamilton, 1891/2. ENFIELD?, BMNH, 20, L, Forbes?, broken. GLENMARK/WEST, CM, AV 5104pt, F R Fuller, 1871, "TYPE", part of type series. CM, AV 5104pt (Fig. 6.3), "TYPE" "44", part of type series. CM, AV5104pt, Haast party, 1873. HAMILTON, AIM , 574pt, B S Booth? F W Hutton. HAMILTON SWAMP?, AIM, 574pt, B S Booth? F W Hutton. AR 144, NMNZ, S 23611pt. GRAVEYARD, NMNZ, S 22712.2, R, P R Millener, 4 Apr 1983. MARFELLS BEACH, CM, AV 11486, R J Scarlett, 26 Jul 1952. CM, AV 11515, R J Scarlett, Jul 1952. CM, AV 11700, J Britton, Nov 1952. CM, AV 12153, J Britton, Jan 1953, part. CM, AV 22268pt, J & R Britton, "1950s". CM, AV 22268pt, J & R Britton, "1950s". MOUNT OWEN (SO 209), S 27773, all phalanges, both 1st metatarsals, both feet, D Smith, T H Worthy, P R Millener, Jan 1990, part of complete skeleton. OREPUKI, SM, A 46.25, Alex King, 1945-46. SM, A 46.26, Alex King, 1945-46. SM, A 46.27, Alex King, 1945-46. SM, A 46.28, Alex King, 1945-46. SM, A 46.29, Alex King, 1945-46. WAIPAPAPA = WAIPAPA POINT, NMNZ, DM 7074, A Hamilton?, tip broken. WAIRAU BAR, CM, AV 12354, J R Eyles, 1942. S 29/2?, CM, AV 36337, N2416.

6.5.9 Remarks. In most respects, Haast's Eagle is a typical aquilin. The main points of difference are those associated with the increase in size. For example, to maintain a head length of normal accipitrid proportions, the proximal section of the bill is elongated, and the angles between the bony struts, and the strut width, are altered so as to maintain sufficient strength.

In the postcranial skeleton, the main differences are in the wing bone lengths and the hypertrophy of the pelvis. The ilio-ischiadic bend is the greatest of any accipitrid. The lower legs, toes, and claws are extremely robust, but similar in morphology and proportions to those in *Aquila*.

Haast's Eagle is separated morphologically from the aquilins by features associated with flapping flight, rather than soaring, and with catching and subduing large prey.

Table 6.1 Dimensions of crania and premaxillae of *Harpagornis moorei*. L, length; PML, premaxilla length; PMW, premaxilla width; POW, postorbital width; IOW, interorbital width; WTF, width across temporal fossae; WSQ, width across squamosal processes; CRD, cranial depth. See Fig. 4.1 for measurement landmarks.

Number	Site	L	PML	PMW	POW	IOW	WTF	WSQ	CRD
93.1.30.1?	Enfield	-	-	-	-	28.1+	-	-	-
AV 5684	Pyramid	161.5	87.0	21.4	70.8	26.9	52.2	67.3	50.0
AV 5685	Pyramid	160.0	85.0	21.2	72.4	26.5	51.0	68.4	-
AV 9554	Holyoake	-	-	-	65.9	25.4	48.7	61.1	-
AV 34466	Cannibal	-	-	-	68+*	23.5	50.6	-	-
DM 2134pt	Castle	165.5+	91.0	-	76.0	26.3	53.7	69.0	48.5
S 23473.1	Eagles	152.1	80.1	20.1	66.3	24.2	48.7	61.9	45.4
S 22712.1	Eagles	-	-	-	-	-	-	-	-
S 23479	His	150.5	75.7	19.5	68.5	27.9	48.6	61+*	45.9
S 23611pt	AR144	166.9	90.3	23.8	72.0	28.3	49.7	66.6	47.4
S 23825pt	Graves	-	-	18.7	-	-	-	-	-
S 23825pt	Graves	-	-	20.4	-	-	-	-	-
S 23825pt	Graves	-	-	-	68.3	24.1	48.9	59+*	-
S 25580	Eagles	164.7	87.5	21.0	72.0	26.7	51.2	70.2+	-
S 27773	Mt Owen	164.3	86.5	22.1	70.7	26.1	51.3	65.5±*	45±*
C 40.8	Castle	151.2	69.6	19.4	69.4	24.2	50.0	64.5*	44.6
DM2146pt	Misident								
	n measured	9	9	10	11	13	12	7	7
	Range Low	150.5	69.6	18.7	65.9	23.5	48.6	61.1	44.6
	High	166.9	91.0	23.8	76.0	28.3	53.7	70.2	50.0
	Mean	159.6	83.6	20.8	70.2	26.0	50.4	66.4	47.1
	SD	6.611	7.137	1.489	2.939	1.624	1.592	3.521	1.925
	SE_{mean}	2.204	2.379	0.471	0.886	0.450	0.460	1.331	0.728
	CV (%)	4.14	8.53	7.17	4.19	6.24	3.16	5.31	4.08
	Total seen	16							
	MNI	16							
	Sites	16							

Table 6.2A Dimensions of mandibles of *Harpagornis moorei*. See Table 6.2B (next page) for other dimensions. L, length; W, width; SL, length of symphysis; WA, width of articular process; DA, depth at anterior end of articular process. See Fig. 4.1 for dimension landmarks.

Number	Site	L	W	SL	WA	DA
[BMNH]	Enfield Swamp	126.5±	77.6	27.5	-	-
AV 5323pt	Hamilton Swamp	116.0	71.3	24.9	26.5	9.0
AV 5685pt	Pyramid Valley	124.0	74.1	26.4+	28.1	10.0
AV 12152	Marfells Beach	-	-	20.7	-	-
AV 12355	Pyramid Valley	116.7	67.1	26.8	25.5	9.0
DM 2134	Castle Rocks	126.5	73.5	24.0	28.9	10.3
S 22765	Graveyard	129++*	-	-	28.5	-
S 23480pt	His Cave	-	-	23.9	-	-
S 23480pt	His Cave	-	-	25.2	-	-
S 23611	AR 144	130.8	75.4	28.4	28.6	10.0
S 23825pt	Graveyard	-	-	-	26.8	9.8
S 23825pt	Graveyard	-	-	-	27.4	9.9
S 27773	Mount Owen	124.2	72.1	27.6	29.2	10.3
C 40.8	Castle Rocks	116.7	-	25.3	25.7	-
	n measurable	8	7	11	10	8
	Range Low	116.0	67.1	20.7	25.5	9.0
	High	130.8	77.6	27.6	29.2	10.3
	Mean	122.7	73.0	25.5	27.5	9.8
	SE_{mean}	1.961	1.262	0.658	0.424	0.183
	CV (%)	4.52	4.47	8.56	4.87	5.28
	Total seen	14				
	MNI	14				
	Sites	9				

Table 6.2B Dimensions of mandibles of *Harpagornis moorei*, continued from Table 6.2A. DS, depth at symphysis; TC, tip to coronoid process; TS, tip to surangular process; DSUR, depth at surangular process. See Fig. 4.1 for measurement landmarks.

Number	Site	DS	TC	TS	DSUR
[BMNH]	Enfield Swamp	-	-	-	-
AV 5323pt	Hamilton Swamp	13.4	99.8	96.5	9.5
AV 5685pt	Pyramid Valley	15.0	101.4	97.8	8.4±
AV 12152	Marfells Beach	-	-	-	-
AV 12355	Pyramid Valley	13.6	99.4	95.8	8.0
DM 2134	Castle Rocks	15.5	105.9	101.0	9.9
S 22765	Graveyard	-	-	-	-
S 23480pt	His Cave	-	-	-	-
S 23480pt	His Cave	-	-	-	9.9
S 23611	AR 144	15.3	111.7	107.1	10.2
S 23825pt	Graveyard	15.0	-	-	-
S 23825pt	Graveyard	14.9	-	-	-
S 27773	Mount Owen	14.8	103.8	100.1	8.9
C 40.8	Castle Rocks	-	-	-	-
	n measurable	8	6	6	8
	Range Low	13.4	99.4	95.8	7.6
	High	15.5	111.7	107.1	10.2
	Mean	14.7	103.7	99.7	9.0
	SE_{mean}	0.272	1.896	1.690	0.356
	CV (%)	5.23	4.48	4.15	11.17
	Total seen	14			
	MNI	14			
	Sites	9			

Table 6.3 Dimensions of sterna of *Harpagornis moorei*. L, length; Wstc, width over sternocoracoidal processes; Wprox, anterior width; Dtot, total depth; Dant, depth over anterior margin; Lcar, length of keel; Wpst, posterior width. See Fig. 4.1 for measurement landmarks.

Number	Site	L	Wstc	W prox	Dtot	Dant	Lcar	Wpst
[BMNH]	Enfield?	-	-	-	-	-	-	-
AV 6012/6177	Pyramid	136++*	63.1	86.0+	71.3+	56.0	-	-
AV 6177	Pyramid	-	-	-	-	47.4	-	-
AV 15965	Glenmark?	-	-	-	-	-	-	-
AV 24887pt	Rifle Butts	-	-	-	-	-	-	-
DM 2134pt	Castle Rocks	163.0	88.5	89.6	71.7	54.5	126.0	-
S 22473.2	Eagle Roost	140.5	83.1+	84.8+	65.7	53.9	110.3	55.2
S 22473.3	Eagle Roost	167.2	93.9	96.7	77.4	63.8±	136.2	64.8
S 23051.1	Graveyard	-	-	83±*	-	55.7+	-	-
S 27773	Mount Owen	155.1+	89±*	65.5+*	57±	-	117±*	59.1
C 03.61	Ngapara	-	-	-	-	-	-	-
C 40.8	Castle Rocks	140.3	84.2	83.5	-	-	-	-
A/3 [OMNZ]	Ngapara?	-	-	-	-	-	-	-
	n measurable	5	5	5	4	6	3	3
	Range Low	140.3	63.1	83.5	57.5	47.4	110.3	55.2
	High	167.2	93.9	96.7	77.4	63.8	136.2	64.8
	Mean	153.2	82.6	88.1	71.5	55.2	124.2	59.7
	SD	12.484	11.679	5.290	4.779	5.251	13.047	4.828
	SE_{mean}	5.583	5.223	2.366	2.390	2.144	7.533	2.787
	CV (%)	8.15	14.15	6.00	6.68	9.51	10.51	8.09
	Seen	13						
	MNI	13						
	Sites	9						

Table 6.4 Dimensions of pelves of *Harpagornis moorei*. L, total length; Pw, proximal width; Ww, width at waist; Wint, width across acetabulae; Wpo, posterior width; Wis, width across posterior ilio-ischiadic crest. See Fig. 4.1 for measurement landmarks.

Number	Site	L	Pw	Ww	Wint	Wpo	Wis
75.12.15.34	Obelisk	183.8	58.4	39.8	58.5	82.0	59.4
A 424	Enfield?	-	-	-	-	-	-
AV 5102pt	Glenmark/E	-	-	-	-	-	-
AV 5332 [cast]	'Nelson'	-	-	-	-	-	-
DM 2134pt	Castle Rocks	197.5	66.5±	40.8	61.9	91.6	-
S 22473.4	Eagle Roost	165±	52.4+	33.7	52.8	76.2+	78.3±
S 22473.5	Eagle Roost	190±*	-	42.7	59.8	87.8+	94.5+
S 23030pt	Graveyard	157.0+	55.5	36.1	50.7	76.5	-
S 23460	His Cave	-	-	-	-	-	-
S 23461	His Cave	-	-	-	-	-	-
S 23664	Graveyard	-	-	-	-	-	-
S 27773	Mount Owen	182±*	50±*	35.6±	56.1	86±*	81±*
C 40.8	Castle Rocks	165.5	-	33.1	65.4*	75.4	-
	n measurable	6	3	6	6	4	3
	Range Low	157.0	52.4	33.1	50.7	75.4	59.4
	High	197.5	66.5	42.7	61.9	91.6	94.5
	Mean	173.8	58.2	37.4	56.6	81.6	77.4
	SD	16.509	6.051	3.709	4.276	6.815	17.567
	SE_{mean}	7.383	3.026	1.402	1.746	2.782	10.142
	CV (%)	9.50	10.40	9.92	7.55	8.35	22.7
	Total seen	12					
	MNI	12					
	Sites	8					

Table 6.5 Dimensions of coracoids of *Harpagornis moorei*. S, side; L, length; Wf, width of furcular facet; Wn, width of neck; Wst, width of sternal facet. See Fig. 4.1 for measurement landmarks.

Number	Site	S	L	Wf	Wn	Wst
None	Shirley Creek	?	-	-	-	-
3 [BMNH]	Enfield?	L	-	-	-	-
4 [BMNH]	Enfield?	R	94.6	-	15.9	36.9
AV 13014	Marfells Beach	L	78.1	22.5+	13.4	32.9
S 22472.2	Eagle Roost	L	106.6	30.7+	17.5	44.3
S 22653	Graveyard	L	96.9+	-	16.8	-
S 23451	His Cave	L	-	-	17.8	-
S 23452	His Cave	L	-	29.8	17.7	-
S 23611pt	AR 144	L	104.4	30.1	17.8	42.6
S 27773pt	Mount Owen	L	-	-	-	-
S 27773pt	Mount Owen	R	97.5	30.0	16.3	41++*
None [THW]	His Cave	L	-	-	-	-
S 23453	His Cave	R	85.0	22.9±*	13.6	31.1+
C 32.82	Ngapara	L	100.6	28.5+	17.4	44.2
C 40.8pt	Castle Rocks	L	89.1	-	-	-
C 40.8pt	Castle Rocks	R	87.8	-	-	-
None [OMNZ]	Ngapara?	L	80.4+*	26.2	14.8	-
AV 5339	?	R	84.8	26.1	14.3	-
DM 2134pt	Castle Rocks	R	106.0	31.4	17.5	45.2+
DM 2146pt	?	R	83.0	25.6	14.0	-
S 22472.3	Eagle Roost	R	88.9	28.3	14.5	34.2+
S 22653pt	Graveyard	R	78.6+	-	14.6	-
None [THW]	His Cave	R	89.3	26.2	15.4	35.6±*
	n measurable		15	12	17	9
	Range Low		78.1	22.5	13.4	31.9
	High		106.6	31.4	17.8	45.2
	Mean		92.2	27.9	15.8	38.1
	SD		9.551	2.647	1.612	5.889
	SE_{mean}		2.446	0.764	0.391	1.963
	CV (%)		10.36	9.47	10.17	15.44
	Total seen		23			
	MNI		19			
	Sites		11+			

Table 6.6 Dimensions of scapulae of *Harpagornis moorei*. L, length; Wh, width of head; Wn, width of neck; Wb, maximum width of blade; Lg, length of glenoid fossa. See Fig. 4.1 for measurement landmarks.

Number	Site	Side	L	Wh	Wn	Wb	Lg
AIM 574pt	Hamilton S	?	-	-	-	-	-
	Glenmark/East	L	-	-	-	-	-
[BMNH] 6	Enfield	L	-	-	-	-	-
[BMNH]	Enfield	R	142.3	27.5	-	19.8	-
AV 5104pt	Glenmark/West	L	-	30.6	11.7	-	19.8+
AV 5104pt	Glenmark/West	R	-	30.1+	12.3	-	20.6
AV 5333pt	Oaro	L	127.0	32.1	11.3	20.7	20.4
DM 2134pt	Castle Rocks	L	133.0	33.6	12.6	20.9	-
DM 2134pt	Castle Rocks	R	133.1	33.3	12.5	22.0	-
S 23051.2	Graveyard	L	116.7	28.3	10.7	17.4	17.7
S 23448	His Cave	L	-	33.0	13.3	-	19.4
S 23446	His Cave	R	-	31.8+	13.7	18.4++*	-
S 23449	His Cave	L	-	25.6+	11.5	-	-
S 23447	His Cave	R	-	28.3+	11.7	-	-
S 23664pt	Graveyard	L	-	-	-	-	-
S 27773	Mount Owen	L	127.0	29.5	11.0	19.8	-
S 27773	Mount Owen	R	-	-	10.6	-	-
C 40.8	Castle Rocks	L	118.9	-	11.5	16.8	14.0
C 40.8	Castle Rocks	R	118.1	-	10.5	16.7	15.9
AV 24887	Old Rifle Butts	R	-	29.2	11.9	-	19.3
A/4 [OMNZ]	Ngapara?	R	-	27.4	10.7	-	-
		n measurable	6	10	10	6	6
		Range Low	116.7	25.6	10.7	16.8	14.0
		High	142.3	33.6	13.3	20.9	20.4
		Mean	127.5	29.7	11.6	19.2	18.4
		SD	9.385	2.622	0.822	1.724	2.350
		SE_{mean}	3.831	0.829	0.260	0.704	0.959
		CV (%)	7.36	8.83	7.07	8.96	12.75
		Total seen	21				
		MNI	14				
		Sites	11				

Table 6.7 Dimensions of furculae of *Harpagornis moorei*. W, overall width; Hdv, dorso-ventral height; Hap, 'height' antero-posteriorly; Wart, width of articular facet. See Fig. 4.1 for measurement landmarks.

Number	Site	W	Hdv	Hap	Wart
4? [BMNH]	Enfield?	-	-	-	-
AV 5335	"Otago"	Cast			
AV 24887pt	Old Rifle Butts	-	-	-	-
DM 2134pt	Castle Rocks	94±*	85.2±*	40.0±*	15.9
DM 2146pt	-	-	-	-	14.5
S 22472.1	Eagle Roost	105.2	81.9	46.8	13.9
S 23450	His Cave	-	-	-	-
S 23611pt	AR 144	107.3	81.0	42.3	14.0
S 23720	Graveyard	-	-	-	-
S 23825pt	Graveyard	93.4±*	63.0	-	14.2
S 27773	Mount Owen	99.6	73.1	33.7	-
C 40.8	Castle Rocks	95.3	-	-	-
[SM]	Orepuki	110.0	76.0	-	-
	n measurable	5	5	3	5
	Range Low	95.3	63.0	33.7	13.9
	High	110.0	85.2*	46.8	15.9
	Mean	103.5	75.0	40.9	14.5
	SD	5.959	7.619	6.640	0.815
	SE_{mean}	2.665	3.407	3.833	0.365
	CV (%)	5.76	10.16	16.22	5.62
	Total seen	13			
	MNI	13			
	Sites	8+			

Table 6.8 Dimensions of humeri of *Harpagornis moorei*. L, length; P, proximal width; D, distal width; S, dorso-ventral shaft diameter at distal end of deltoid crest. See Fig. 4.1 for measurement landmarks. Continued next page.

Number	Site	Side	L	P	D	S
	Albury Park	L	-	-	-	-
BMNH 8	Enfield?	L	228.2	55.6	42.2	17.8
A423 BMNH	"Oamaru"	L	233.3	53.6	43.0	17.5
BMNH 9	Enfield?	R	232.9	54.9	41.4	17.1
AV 5333pt	Oaro	L	231.0	55.0	42.9	17.0
AV 5333pt	Oaro	R	-	-	-	17.3
AV 5587	Pyramid Valley	L	-	-	-	-
AV 29361	Kakanui Beach	L	228.6	58.3	42.0+	18.7
DM 2143	Motunau	L	208.0	47.1	37.1	17.1
DM 2145	Castle Rocks?	L	241.0	49.0+	42.6+	18.0
S 22736	Eagle Roost	L	254.2	57.9+	45.5	20.1
S 25581	Eagle Roost	R	254.3	-	39.5+	19.8
S 23030pt	Graveyard 3	L	240.4	54.4+	43.2+	19.2
S 23431	His Cave	L	249.9	56.9	43.7	20.0
S 23432	His Cave	L	219.8	48.1	37.8	16.7
S 23433	His Cave	L	256.0+	56.6	42.8	20.3
S 23459pt	His Cave	L	-	-	34.0+*	-
S 23459pt	His Cave	R	-	-	-	-
S 23459pt	His Cave	L	-	-	-	-
S 23459pt	His Cave	R	-	-	-	15.7

Table 6.8 continued Dimensions of humeri of *Harpagornis moorei*. L, length; P, proximal width; D, distal width; S, dorso-ventral shaft diameter at distal end of deltoid crest.

Number	Site	Side	L	P	D	S
S 23825pt	Graveyard 3	L	232.0+	54.1+	41.1+	18.7
S 23825pt	Graveyard 3	L	222.7	49.4	39.4	17.3
S 25887	E entrance	L	-	-	-	-
S 27773pt	Mount Owen	L	233.6	56.5	44.4	17.8
S 27773pt	Mount Owen	R	234.0	-	41.6+	17.7
C 40.8pt	Castle Rocks	L	214.5	-	39.3	15.2±*
C 40.8pt	Castle Rocks	R	214.2	-	37.6+	15.9
AV 5102pt	Glenmark/East	R	216.4	49.6	39.0	15.6
AV 9556	Glenmark Creek	R	-	-	-	-
AV 36396	Hives extension	R	259.9	55.7+	47.3+	21.0
DM 2146	-	R	210.3	-	37.4	15.6
S 23825pt	Graveyard 3	R	213.5	42.3+	36.1	16.1
OMNZ A1	Ngapara?	R	-	48.4	-	-
		n measurable	20	18	21/20	21
		Range Low	208	42.3	37.1	15.6
		High	259.9	58.3	47.3	21.0
		Mean	232.4	52.7	41.3	17.9
		SD	16.253	4.526	3.005	1.693
		SE_{mean}	3.634	1.067	0.672	0.369
		CV (%)	6.99	8.59	7.27	9.46
		Total seen	34			
		MNI	26			
		Sites	16+			

Table 6.9 Dimensions of ulnae of *Harpagornis moorei*. L, length; Pdv, proximal dorso-ventral depth; Pap, proximal antero-posterior width; Wd, distal width; Wd1, distal width across margins of trochlea. See Fig. 4.1 for measurement landmarks. Continued next page.

Number	Site	Side	L	Pdv	Pap	Wd	Wd1
[NOM]	Shirley	L	-	-	-	-	-
AU 9723	Shirley	R	263.5	30.8+	21.5+	18.7	21.7
S 23664pt	Graveyard	L	-	-	-	-	-
S 23030pt	Graveyard	R	248.8	26.8	20.3	17.2	20.1
S 23664pt	Graveyard	L	-	-	-	-	-
S 23825pt	Graveyard	R	-	-	-	-	17.6
AV 5102pt	Glenmark/East	L	231.2	25.0	19.0	18.0	21.4
AV 5102pt	Glenmark/East	R	236.1	27.0	20.2	17.4	20.1
AV 5104pt	Glenmark/West	L	-	-	-	-	-
AV 5104pt	Glenmark/West	R	254.4+	-	-	18.7	22.4
AV 5329pt	Enfield	L	247.8	29.2	21.9	19.2	22.0
[BMNH] 13	Enfield?	R	248.8	27.3	-	21.6±*	-
AV 36405	Hives extension	L	279.2	32.2	24.2	21.4	23.8
DM 2134pt	Castle Rocks	L	258.4+	30.8	23.9	23.1	-
DM 2134pt	Castle Rocks	R	261.0	32.1	23.1	23.2	-
S 22476.2	Eagle Roost	L	281.5	32.5+	24.1	20.7	24.1
S 23435	His Cave	L	242.7+	23.8+	18.9	15.7+	-
S 23439	His Cave	L	-	-	-	-	-
S 23434	His Cave	R	249.2	27.3	19.8	17.5	20.0
S 23611pt	AR 144	L	269.1	32.2	23.1	18.9	23.1
S 23611pt	AR 144	R	-	31.6	23.2	-	-
S 27773pt	Mount Owen	L	252.5	29.8	21.7	19.9	23.1
S 27773	Mount Owen	R	251.1+	29.8	22.8	-	22.1+

Table 6.9 continued Dimensions of ulnae of *Harpagornis moorei*. L, length; Pdv, proximal dorso-ventral depth; Pap, proximal antero-posterior width; Wd, distal width; Wd1, distal width across margins of trochlea. See Fig. 4.1 for measurement landmarks.

Number	Site	Side	L	Pdv	Pap	Wd	Wd1
C 40.8pt	Castle Rocks	L	230.4	26.1	19.1	20.5	-
C 40.8pt	Castle Rocks	R	227.2+	26.4	-	20.3	-
[OMNZ]	Hamilton	L	252.2	29.5	21.5	17.5	22.4
AV 9555	Hamilton	R	-	-	-	-	-
AV 5324pt	Hamilton	R	228.1	25.6	19.3	16.9	19.1
S 23436	His Cave	R	268.2+	28.9+	22.0+	19.3	22.3
S 23437	His Cave	R	270.1+	32.6	22.7++*	20.6	23.1
S 23438	His Cave	R	271.3	30.2	20.9+	20.4	-
S 23825pt	Graveyard	R	244.5	26.6	19.6	-	20.0
S 23825pt	Graveyard	R	-	-	-	-	23.0
		n measurable	20	19	17	19	17
	Range	Low	228.1	23.8	18.9	15.7	17.6
		High	281.5	32.6	24.2	23.2	24.1
		Mean	254.4	29.0	21.2	19.1	21.7
		SD	15.786	2.718	1.827	1.784	1.773
		SE_{mean}	3.530	0.624	0.443	0.409	0.430
		CV (%)	6.21	9.38	8.61	9.32	8.17
		Total seen	34				
		MNI	22				
		Sites	13				
plus ulnae used for artefacts at Wairau and Sumner							

Table 6.10 Dimensions of radii of *Harpagornis moorei*. L, length; Pw, proximal width; Dw, distal width. See Fig. 4.1 for measurement landmarks.

Number	Site	Side	L	Pw	Dw
[BMNH] 14	Enfield?	L	232.2	-	-
[BMNH]	Enfield?	R	232.9	-	-
[BMNH] A 423pt	Enfield	L	223.8	-	-
AV 5104pt	Glenmark/West	L	-	-	-
AV 5104pt	Glenmark/West	R	217.6	12.6	16.3
AV 24887pt	Old Rifle Butts	L	-	-	-
AV 24887pt	Old Rifle Butts	R	-	-	-
S 23443	His Cave	L	-	-	-
S 23442	His Cave	R	-	-	-
S 27773	Mount Owen	L	237.2	14.9	19.7
S 27773	Mount Owen	R	-	-	-
03.61	Ngapara	L	-	-	-
C 40.8pt	Castle Rocks	L	211.7	-	-
C 40.8pt	Castle Rocks	R	212.5	-	-
AV 5329pt	Enfield	R	233.6	14.1	17.6
AV 5333pt	Oaro	R	231.5	14.3	18.9
DM 2134pt	Castle Rocks	R	245.4	15.5	18.7
S 23073.2	Graveyard	R	229.4	11.9	15.4
S 23440	His Cave	R	257.2	14.3	19.5
S 23441	His Cave	R	-	-	-
S 23443	His Cave	R	-	-	-
S 23472.4	Eagle Roost	?	263.5	16.6	-
S 23825pt	Graveyard 3	?	223.8	11.2	14.8
S 23051.4	Graveyard terrace	?	-	-	-
S 23051.5	Graveyard terrace	?	-	-	-
S 23445	His Cave	?	-	-	-
	n measurable		13		
	RangeLow		211.7		
	High		263.5		
	Mean		235.7		
	SD		15.955		
	SE_{mean}		4.425		
	CV (%)		6.77		
	Total seen		27		
	MNI		19±		
	Sites		10		

Table 6.11 Dimensions of carpometacarpi of *Harpagornis moorei*. L, length; P, proximal width; D, distal width. See Fig. 4.1 for measurement landmarks. Continued next page.

Number	Site	Side	L	P	D
AIM 574	Hamilton	L	-	-	-
[BMNH] R 3184	Enfield	L	117.8	32.8	21.3
BMNH 36	Enfield?	L	118.9	31.3	22.7
BMNH 36	Enfield?	R	120.4	32.0	23.0
AV 5102pt	Glenmark/East	L	113.1+	29.4	20.2
AV 6291	Hamilton?	L	105.9	28.4	19.4
AV 11163	Marfells Beach	L	106.0	-	18.1
DM 2134pt	Castle Rocks	L	125.4	33.7	20.9
DM 2134pt	Castle Rocks	R	123.0	33.4	19.7
DM 2143pt	Motunau	L	-	-	19.3
S 22472.7	Eagle Roost	L	131.4	34.5	21.3+
S 22472.8	Eagle Roost	R	131.8	34.8	24.9
S 23454	His Cave	L	-	33.4	-
S 23458	His Cave	R	-	29.2+	-
S 23455	His Cave	L	123++	-	-
S 23456	His Cave	R	124.6+	29.5+	-
S 23611pt	AR 144	L	127.2	34.0	22.9
S 23664pt	Graveyard 1	L	-	-	-
S 22653	Graveyard channel	R	115.3	29.4	20.8

Table 6.11 continued Dimensions of carpometacarpi of *Harpagornis moorei*. L, length; P, proximal width; D, distal width. See Fig. 4.1 for measurement landmarks.

Number	Site	Side	L	P	D
S 23825pt	Graveyard 3	L	122.3	31.7+	22.1
S 25882	Hives extension	L	106.8	28.6+	20.1+
S 27773pt	Mount Owen	L	124.9	33.8	23.3
S 27773pt	Mount Owen	R	123.9+	33.8	22.8
C 40.8pt	Castle Rocks	L	105.5	25.1	-
C 40.8pt	Castle Rocks	R	108.4	-	-
C 32.81	Ngapara	L	117.9+	33.9+	-
AV 22481	Kings Cave	R	-	-	-
S 23457	His Cave	R	113.1+	26.4+	19.4
		n measurable	16	16	14
		Range Low	105.5	25.5	18.1
		High	131.8	34.8	24.9
		Mean	117.3	31.0	21.1
		SD	8.359	2.947	1.883
		SE_{mean}	2.090	0.737	0.503
		CV (%)	7.13	9.51	8.93
		Total seen	28		
		MNI	20		
		Sites	15		

Table 6.12 Dimensions of femora of *Harpagornis moorei*. L, length; PrW, proximal width; DistW, distal width; Ssag, mid-shaft sagittal diameter; Smed, mid-shaft medial diameter of shaft. See Fig. 4.1 for measurement landmarks. Continued on next page.

Number	Site	Side	L	PrW	DistW	Ssag	Smed
AU 9723pt	Shirley	L	162.5	44.2	46.7	19.3	19.3
AU 9723pt	Shirley	R	163.2	43.4	46.1	19.2	19.4
BMNH 10	Enfield?	L	163.8	40.4	45.6	18.4	19.7
BMNH 11	Enfield?	R	163.1+	44.4+	46.5+	18.8	19.9
AV 24887pt	Old Rifle Butts	L	-	-	38.5+	-	-
AV 28366	Pyramid Valley	L	175.8	46.1	52.6	19.9	20.7
AV 5102pt	Glenmark/East	L	153.3	-	36.2+	17.0	17.3
AV 5102pt	Glenmark/East	R	154.5	38.3	39.4+	16.4	17.2
AV 5104pt	Glenmark/West	L	166.9	44.5	48.1	19.0	19.9
DM 2138	-	L	171.3	46.4	49.0	19.6	22.2
S 22472.9	Eagle Roost	L	174.7	47.5	51.8	19.7	20.4
S 22472.10	Eagle Roost	R	176.0	47.4	50.7+	19.7	20.3
S 23030pt	Graveyard 3	L	163.9	41.1+	45.7±	18.4	19.1
S 23462	His Cave	L	169.2+	-	45.2+	18.9	20.1
S 23463	His Cave	R	169.7+	-	41.6+	18.6	19.7
S 23464	His Cave	L	149.5+	-	-	15.3	15.8
S 23465	His Cave	L	-	42.3+	-	19.4±	-
S 27773pt	Mount Owen	L	170.4	45.9	48.6	19.1	20.3
S 27773pt	Mount Owen	R	171.0	46.4	48.2	19.4	20.2

Table 6.12 continued ·Dimensions of femora of *Harpagornis moorei*. L, length; PrW, proximal width; DistW, distal width; Ssag, mid-shaft sagittal diameter; Smed, mid-shaft medial diameter of shaft. See Fig. 4.1 for measurement landmarks.

Number	Site	Side	L	PrW	DistW	Ssag	Smed
C 40.8pt	Castle Rocks	L	151.4	37.3	42.3	16.9	17.4
C 40.8pt	Castle Rocks	R	150.5	37.2	44.1	17.1	17.5
OMNZ	Hamilton Swamp	L	145+ + *	39.1	-	16.9	17.3
AV 9651	Marfells Beach	R	152+ + *	-	43.4	16.1	16.7
DM 2143pt	Motunau	R	140.3	36.0	36.6	15.5	16.4
DM 2145pt	-	R	174.5	40.6	51.2	19.4	20.9
S 23611pt	AR 144	R	170.9	46.7	49.1	19.9	20.4
S 23825pt	Graveyard 3	R	159.4	43.7	-	-	-
S 23625pt	Graveyard 3	R	150.1	37.0	40.5	-	-
		n measurable	17	17	17	18	17
		Range Low	140.3	36.0	36.2	15.3	15.8
		High	147.5	47.5	52.6	19.9	22.2
		Mean	162.82	42.18	45.36	18.26	19.05
		SD	10.546	3.775	5.122	1.552	1.863
		SE_{mean}	2.558	0.916	1.242	0.369	0.452
		CV (%)	6.48	8.95	11.29	8.50	9.78
		Total seen	29				
		MNI	22				
		Sites	16				

Table 6.13 Dimensions of tibiotarsi of *Harpagornis moorei*. S, side; L, length; Pw, proximal width; Dw, distal width; Ssag, mid-shaft sagittal diameter; Smed, mid-shaft medial diameter; Dd, distal depth; Fib, proximal to distal fibular insertion. See Fig. 4.1 for measurement landmarks. Continued on next page.

Number	Site	S	L	Pw	Dw	Ssag	Smed	Dd	Fib
NOM	Shirley	?	-	-	-	-	-	-	-
BMNH 16	Enfield?	L	236.8	43.7	34.2	14.9	18.1	-	-
BMNH 15	Enfield?	R	239.6	43.1	34.1	14.9	18.2	-	-
BMNH A 2119	Hamilton Swamp	L	-	-	-	-	-	-	-
AV 5324	Hamilton Swamp	R	208++*	38.8	29.2	12.5	15.5	-	-
AV 11041	Marfells Beach		-	-	-	-	-	-	-
AV 5102pt	Glenmark/East	L	219++*	-	29.4	13.1	15.7	-	-
AV 5102pt	Glenmark/East	R	219++*	-	30.1	13.0	15.4	-	-
AV 5104pt	Glenmark/West	L	239.8+	47.4	34.5	15.4	18.1	-	95.8
AV 5104pt	Glenmark/West	R	242.1	47.1	35.0	15.5	18.0	-	101.3
AV 5333pt	Oaro	L	236.8	47.4	35.6	14.4	18.0	-	98.4
DM 2143pt	Motunau	L	-	-	29.7	-	-	-	-
DM 2146pt	Te Aute?	L	-	-	-	-	-	-	-
S 22472.11	Eagle Roost H	L	253.9	50.9	39.8	15.7	18.7	-	-
S 22473.6	Eagle Roost G	R	255.1	51.7	39.3	15.7	18.5	-	100.1
S 22653pt	Graveyard 3	L	-	-	34++*	-	-	-	-
S 23467	His Cave	L	247.2+	45.0	33.3	15.8	18.0	-	98.8
S 23468	His Cave	R	240++	-	33.9+	15.8	18.0	-	-
S 23470	His Cave	L	216.4+	-	-	12.1	14.4	-	-
S 23825pt	Graveyard 3	L	-	-	-	-	-	-	-
S 27773pt	Mount Owen	L	241.1	48.8	37.3	15.3	18.1	-	94.1
S 27773pt	Mount Owen	R	239.4+	48.3	35.7+	15.1	17.5	-	96.9

Table 6.13 continued Dimensions of tibiotarsi of *Harpagornis moorei*. L, length; Pw, proximal width; Dw, distal width; Ssag, mid-shaft sagittal diameter; Smed, mid-shaft medial diameter; Dd, distal depth; Fib, proximal to distal fibular insertion. See Fig. 4.1 for measurement landmarks.

Number	Site	S	L	Pw	Dw	Ssag	Smed	Dd	Fib
C 40.8pt	Castle Rocks	L	221.1	32.2	36.5	-	15.9	-	-
C 40.8pt	Castle Rocks	R	221.3	-	31.7	12.6	16.0	-	-
AV 5322	Kapua	R	213.1	-	30.1	11.8	14.6	-	-
DM 2134pt	Castle Rocks	R	247.2	46.5	38.3	15.1	18.8	-	-
DM 2144	Te Aute no. 2	R	-	-	27.3	-	-	18.1	-
DM 2145	-	R	-	-	38.4	-	-	-	-
S 23466	His Cave	R	223+ +*	-	27+ +*	-	-	-	-
S 22473.7	Eagle Roost G	R	228.0	42.2	30.4	12.6	15.1	-	90.2
S 23469	His Cave	R	245+ +*	48.5	35.8	16.6	18.2	-	-
S 23471	His Cave	R	-	-	-	16±*	18±*	-	-
S 23611pt	AR 144	R	243.2	44.6	39.2	15.0	17.5	-	79.0
-	Albury Park	R	-	-	-	-	-	-	-
		n measurable	17	15	15	17	16		
		RangeLow	213.1	32.2	27.3	11.8	14.4	15.7	79.0
		High	255.1	51.7	39.8	16.6	18.8	18.1	101.3
		Mean	235.58	44.6	34.06	14.19	16.98		94.5
		SD	13.074	5.10	4.015	1.572	1.575		7.79
		SE_{mean}	3.774	1.47	0.974	0.406	0.407		2.94
		CV (%)	5.55	11.4	11.79	11.07	9.27		8.24
		Total seen	33						
		MNI	26						
		Sites	18						

Table 6.14A Dimensions of tarsometatarsi of *Harpagornis moorei*. L, length; P, proximal width; D, distal width. See Fig. 4.1 for measurement landmarks. Continued on next page.

Number	Site	Side	L	P	D
BMNH 19	Enfield?	L	153.2	37.4	42.8
BMNH	Enfield?	R	153.4	37.7	39.8
AV 12263	Marfells Beach	L	138.4	31.1	34.4
AV 16221	Marfells Beach	L	135±*	-	36.4
AV 29361pt	Kakanui Beach	L	-	-	-
AV 5102pt	Glenmark/East	L	147.7	31.4	36.4
AV 5102pt	Glenmark/East	R	147.6	30.7+	36.4
AV 5104pt	Glenmark/West	L	154.8	36.9	40.6
AV 5104pt	Glenmark/West	R	153.6	33.0+	41.2
DM 2134pt	Castle Rocks	L	160.8	38.9	43.4
DM 2137	Warrington	L	137.0	30.2	35.6
S 22472.14	Eagle Roost H	L	164.9	40.0	43.6
S 22473.8	Eagle Roost G	R	166.4	40.2	44.6
S 23473	His Cave	L	143.8	28.8+	34.3
S 23472	His Cave	R	144.8	29.3	33.8
S 23474	His Cave	L	145.7	31.0	35.7
S 23475	His Cave	L	157.9	-	38.2+
S 23720pt	Graveyard 1	L	-	-	-
S 23073.1	Graveyard 1	R	144.1	31.5	33.8
S 23825pt	Graveyard 3	L	139±*	29±*	-
S 23825pt	Graveyard 3	L	145.8+	-	-
S 23825pt	Graveyard 3	R	-	-	-
S 27773pt	Mount Owen	L	154.5	38.0	43.6
S 27773pt	Mount Owen	R	154.0	38.0	43.6

Table 6.14A Continued Dimensions of tarsometatarsi of *Harpagornis moorei*. L, length; P, proximal width; D, distal width. S ee Fig. 4.1 for measurement landmarks. Continued on next page.

Number	Site	Side	L	P	D
C 40.8pt	Castle Rocks	L	141.4±*	32.2	36.5
C 40.8pt	Castle Rocks	R	141.8	31.9	37.1
C 32.83pt	Ngapara	L	153.8	38.2	43.4
C 32.83pt	Ngapara	R	-	-	-
93.1.30.21	Motunau	R	139.6	30.0	37.6
AV 5329pt	Enfield	R	152.6	37.1	42.1
AV 36397	Hives extension	R	-	-	-
DM 2136	Dunstan Range	R	157.0	37.9	42.7
DM 2139	-	R	148.0+	36.3+	38.5+
DM 2143pt	Motunau	R	131.5	28.3	33.1
S 23477	His Cave	R	-	28.3+	-
S 23664pt	Graveyard 1	R	-	-	42.0+
C 03.60	Ngapara	R	138.9	30.1	36.8
NOM	Shirley	L	-	-	-
NOM	Shirley	R	-	-	-
	n measurable		21	20	22
	RangeLow		131.5	28.3	33.1
	High		166.4	40.2	44.6
	Mean		148.2	33.7	38.7
	SD		8.713	4.029	3.674
	SE_{mean}		1.901	0.901	0.783
	CV (%)		5.88	11.93	9.49
	Total seen		40		
	MNI		28		
	Sites		17±		

Table 6.14B Dimensions of tarsometatarsi of *Harpagornis moorei*: details of trochleae. Din, depth of medial hypotarsal ridge; Den, depth of lateral hypotarsal ridge; Dint, depth of bone between hypotarsal ridges; Dd, distal depth; Met, proximal end to proximal margin of metatarsal facet. See Fig. 4.1 for measurement landmarks. Continued on next page.

Number	Site	Side	Din	Den	Dint	Dd	Met
BMNH 19	Enfield?	L	-	-	-	25.4	-
BMNH	Enfield?	R	-	-	-	25.4	-
AV 12263	Marfells Beach	L	22.9	20.4	13.1	18.5	-
AV 16221	Marfells Beach	L	-	-	-	19.1	-
AV 29361pt	Kakanui Beach	L	-	-	-	-	-
AV 5102pt	Glenmark/East	L	25.1	21.5	13.7	21.2	103.0
AV 5102pt	Glenmark/East	R	-	-	12.4+	21.2	103.2
AV 5104pt	Glenmark/West	L	17.6	21.6	-	24.7	104.4
AV 5104pt	Glenmark/West	R	-	-	15.3	23.4	-
DM 2134pt	Castle Rocks	L	-	-	15.9	25.4	108.5
DM 2137	Warrington	L	-	-	12.6	18.9	93.6
S 22472.14	Eagle Roost H	L	30.1	24.2	16.4	24.4	-
S 22473.8	Eagle Roost G	R	-	25.5	17.4	24.6	-
S 23473	His Cave	L	-	-	-	18.4+	-
S 23472	His Cave	R	21.7+	18.0+	13.2	19.7	-
S 23474	His Cave	L	24.4	21.2	13.1	19.6	-
S 23475	His Cave	L	-	-	-	22.3+	-
S 23720pt	Graveyard 1	L	-	-	-	-	-
S 23073.1	Graveyard 1	R	22.5	17.8	12.3	18.1	-
S 23825pt	Graveyard 3	L	-	-	11.4	-	-
S 23825pt	Graveyard 3	L	-	-	-	-	-
S 23825pt	Graveyard 3	R	-	-	-	-	-
S 27773pt	Mount Owen	L	29.6	26.1	17.2	25.0	104.4
S 27773pt	Mount Owen	R	29.6	26.1	17.4	24.8	104.0

Table 6.14B Continued Dimensions of tarsometatarsi of *Harpagornis moorei*: details of trochleae. Din, depth of medial hypotarsal ridge; Den, depth of lateral hypotarsal ridge; Dint, depth of bone between hypotarsal ridges; Dd, distal depth; Met, proximal end to proximal margin of metatarsal facet. See Fig. 4.1 for measurement landmarks.

Number	Site	Side	Din	Den	Dint	Dd	Met
C 40.8pt	Castle Rocks	L	-	-	-	-	-
C 40.8pt	Castle Rocks	R	-	-	-	-	-
C 32.83pt	Ngapara	L	29.7	23.2	17.4	25.5	-
C 32.83pt	Ngapara	R	-	-	-	-	-
93.1.30.21	Motunau	R	-	-	-	19.4	-
AV 5329pt	Enfield	R	28.9	25.0	16.3	25.2	102.5
AV 36397	Hives extension	R	-	-	-	-	-
DM 2136	Dunstan Range	R	28.8	24.3	16.8	24.2	103.8
DM 2139	-	R	-	-	-	20.1	-
DM 2143pt	Motunau	R	-	-	11.6	18.9	89.9
S 23477	His Cave	R	-	-	11.3	-	-
S 23664pt	Graveyard 1	R	-	-	-	23.5+	-
C 03.60	Ngapara	R	-	-	-	-	-
NOM	Shirley	L	-	-	-	-	-
NOM	Shirley	R	-	-	-	-	-
		n measurable	11	11	16	20	8
		Range Low	17.6	17.8	11.3	18.1	89.9
		High	30.1	26.1	17.4	25.5	108.5
		Mean	25.6	22.1	14.2	22.0	101.3
		SD	4.147	2.729	2.194	2.808	6.221
		SE_{mean}	1.250	0.823	0.548	0.628	2.199
		CV (%)	16.22	12.34	15.42	12.79	6.14
		Total seen	40				
		MNI	28				
		Sites	17±				

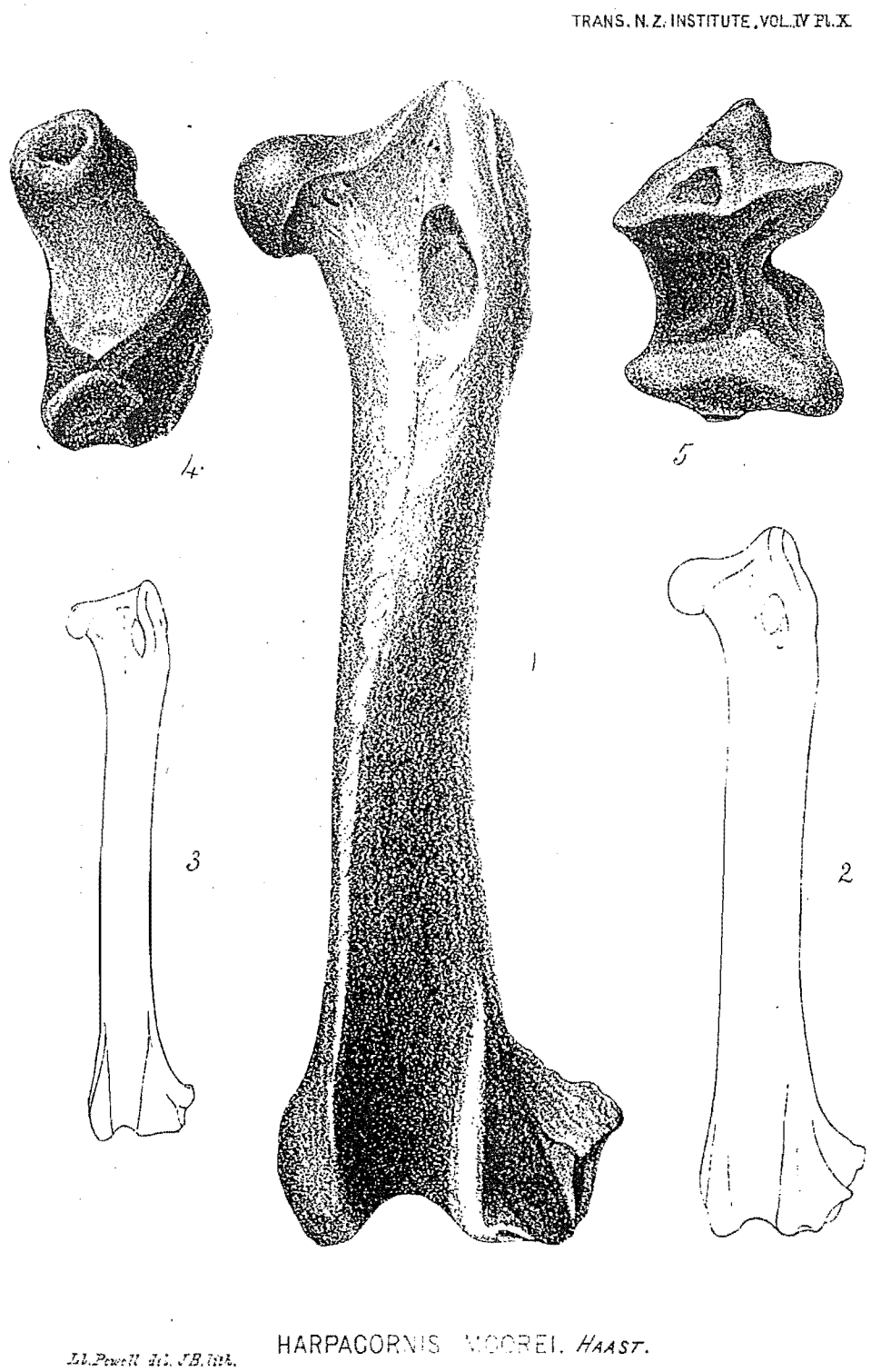


Fig. 6.1A Plate X, accompanying Haast's original description of *Harpagornis moorei* (Haast 1872). Material is now CMNZ AV 5104.

Plate X.—Fig. 1. Femur of *Harpagornis Moorei*, back view of left leg. Fig. 2, Femur of *Poliocætus leucogaster*, back view of left leg. Fig. 3. Femur of *Circus assimilis*, back view of left leg. Fig. 4. Proximal end of femur of *Harpagornis Moorei*, left leg. Fig. 5. Distal end of femur of *Harpagornis Moorei*, left leg.

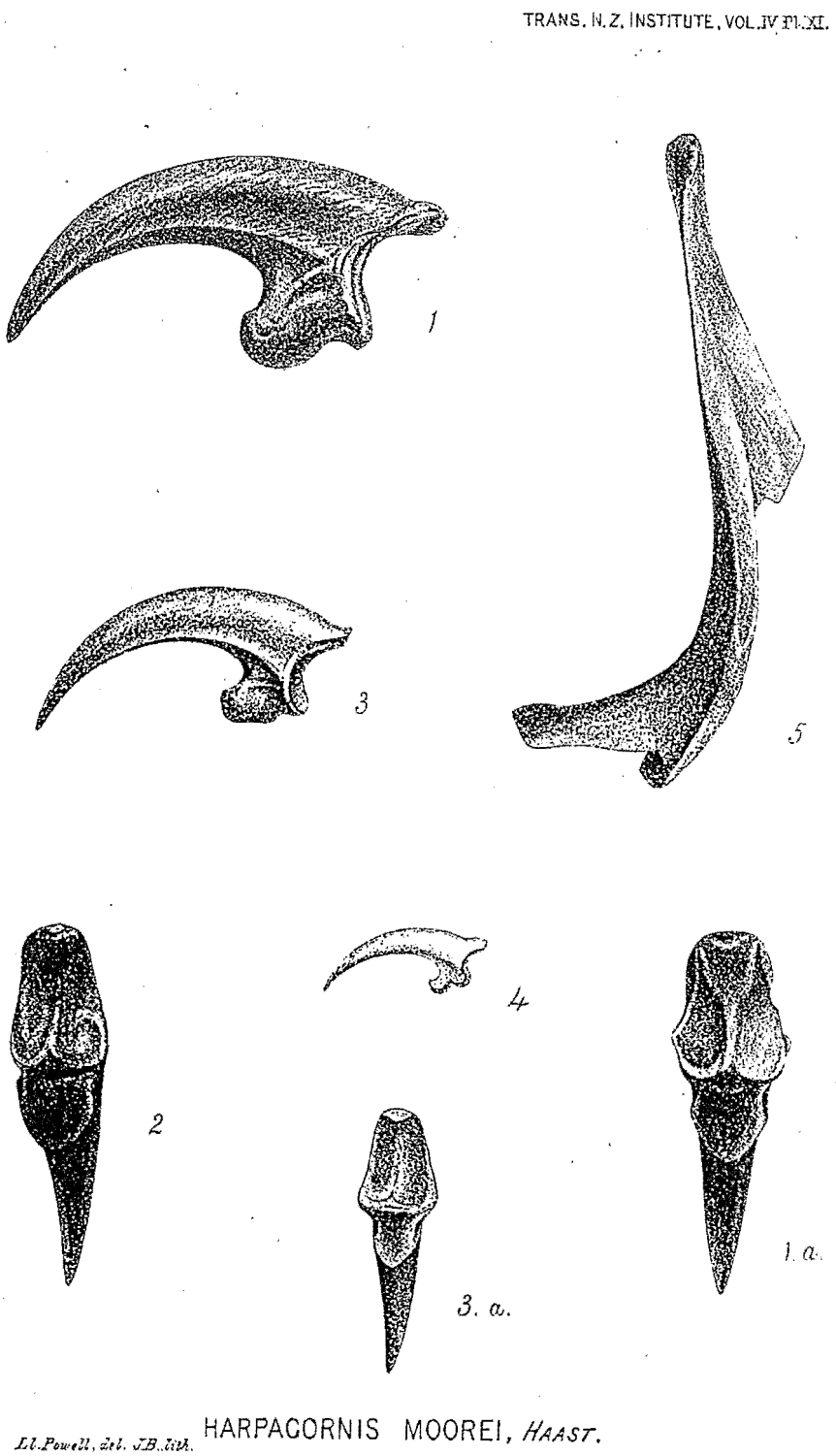


Fig. 6.1B Plate XI, accompanying Haast's original description of *Harpagornis moorei* (Haast 1872). Material is now CMNZ AV 5104.

> Plate XI.—Fig. 1. Ungual phalanx (of hallux, left leg) of *Hapagornis Moorei.* Fig. 1*a*. Proximal articular surface of fig. 1. Fig. 2. Ungual phalanx, probably of second toe of right foot. Fig. 3. Ungual phalanx of hallux, left leg of *Aquila audax.* Fig. 3*a*. Proximal articular surface of fig. 3. Fig. 4. Ungual phalaux of hallux, left leg of *Circus assimilis.* Fig. 5. Third rib right side of *Harpagornis Moorei.*
>
> NOTE.—All these figures are of the natural size.

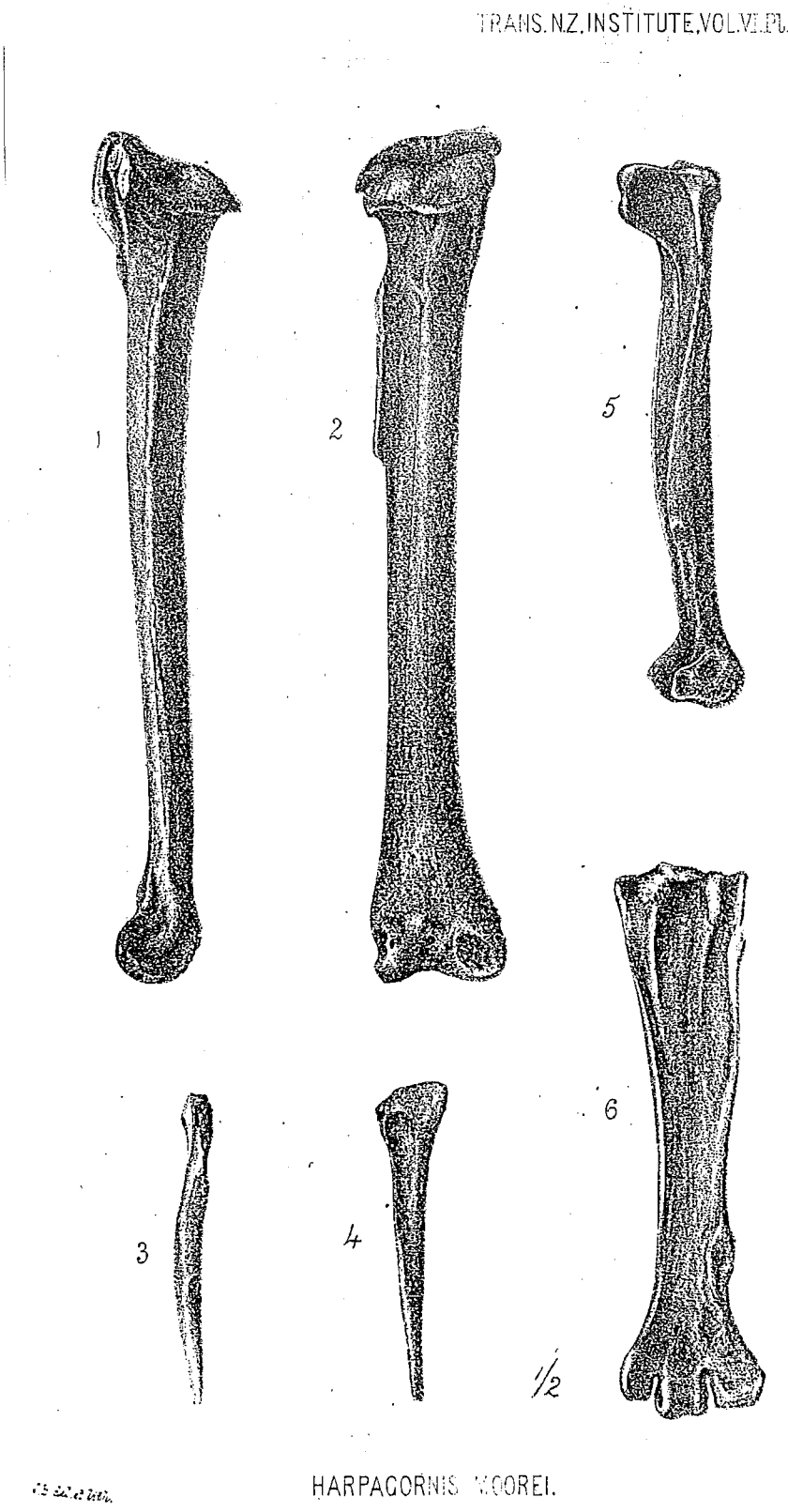


Fig. 6.1C Plate VII, accompanying Haast's description of *Harpagornis assimilis*, and report on further elements from the first individual (Haast 1874). Material now AV 5102, and AV 5104.

DESCRIPTION OF PLATES VII.—IX.

Plate VII.—Figs. 1–2. Tibia of *Harpagornis moorei*.

3–4. ~~Metatarsus~~ „ „ Fibula

5–6. Metatarsus of H. moorei.

Fig. 6.1D Plate VIII, accompanying Haast's description of *Harpagornis assimilis*, and report on further elements from the first individual (Haast 1874). Material now AV 5102, and AV 5104.

VIII.—Figs. 1–2. Humerus of *Harpagornis assimilis.*
3–4. Ulna „ „
5–6. Radius „ „
7. Metacarpus „ „

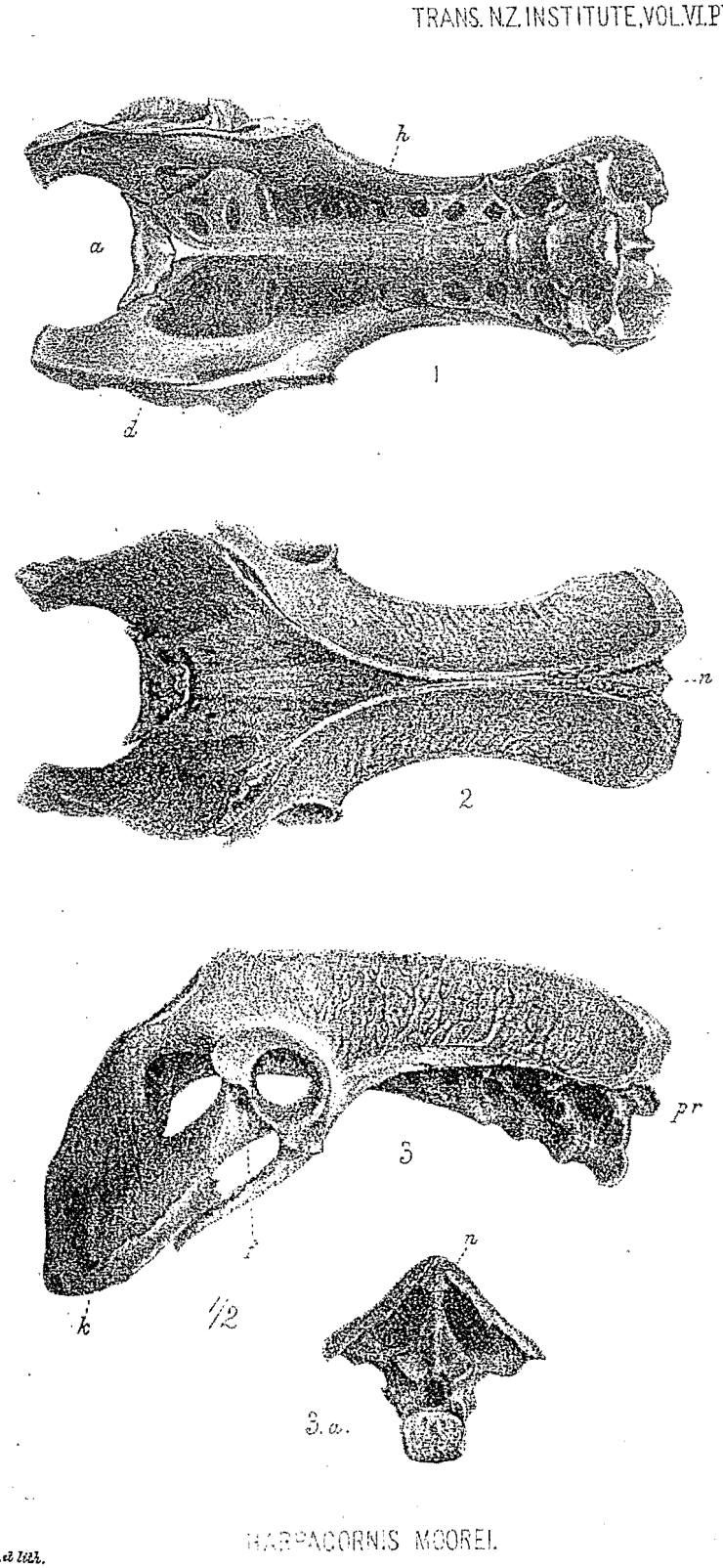


Fig. 6.1E Plate IX, accompanying Haast's description of *Harpagornis assimilis*, and report on further elements from the first individual (Haast 1874). Material now AV 5102, and AV 5104.

IX.—Figs. 1–3. Pelvis of *Harpagornis moorei*.

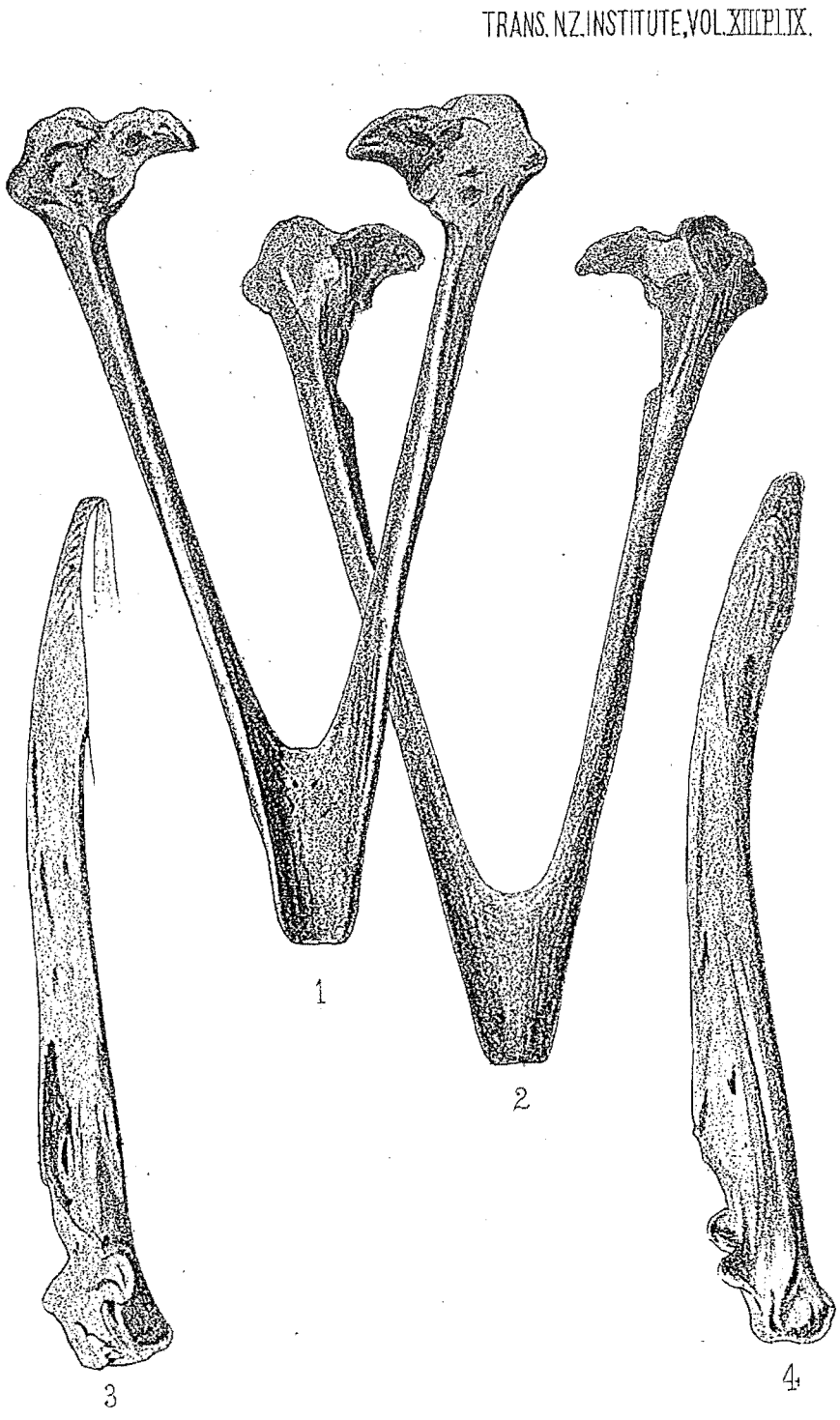


Fig. 6.1F Plate IX, accompanying Haast's description of material of *Harpagornis moorei* and *Harpagornis assimilis* from Hamilton Swamp, Otago (Haast 1881).

DESCRIPTION OF PLATE IX.

1. Upper view of mandible of *Harpagornis assimilis*, von Haast.
2. Lower " " " " "
3. Outside " " " " "
4. Inside " " " " "

All natural size.

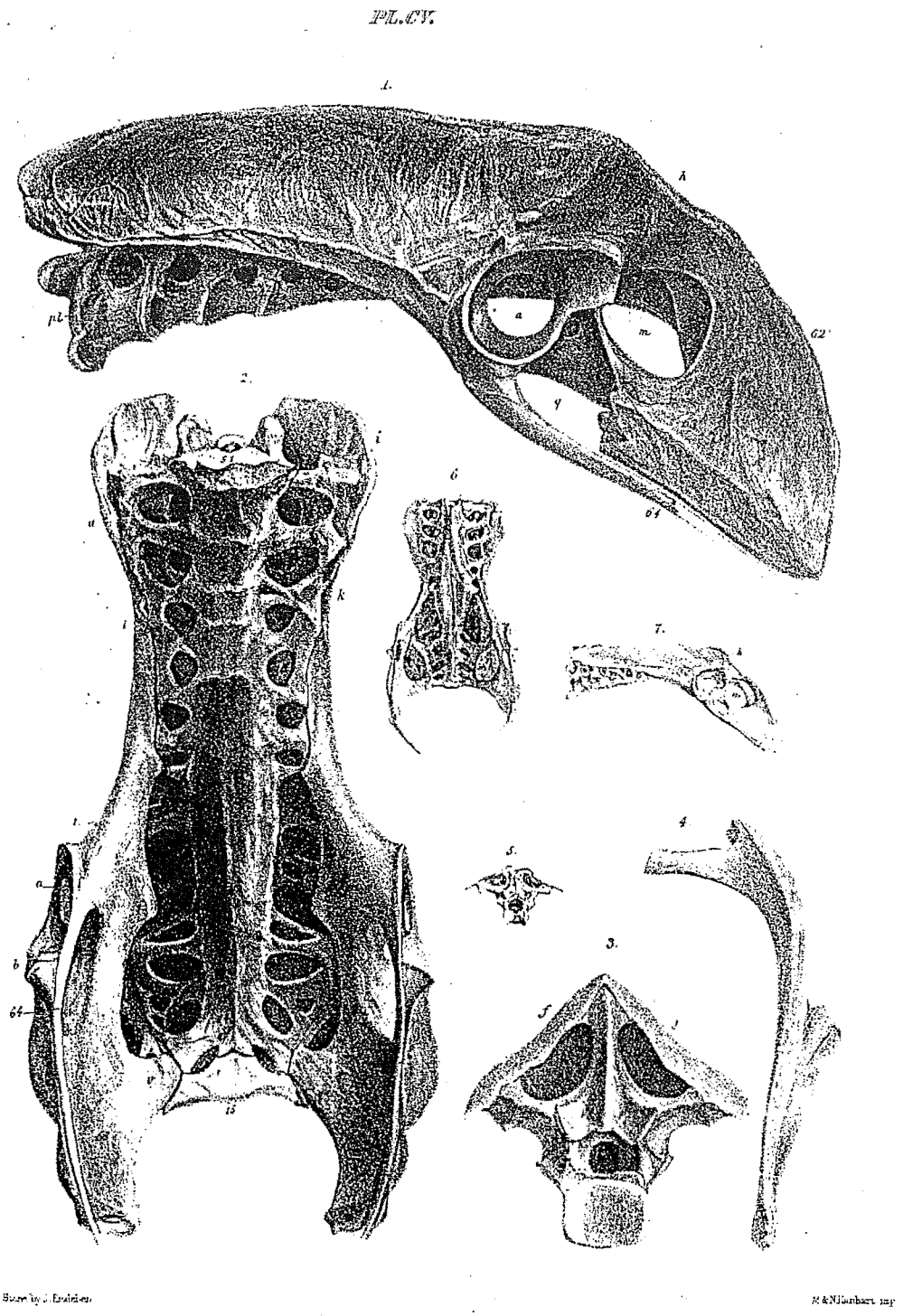


Fig. 6.1G Plate CV, from Vol. 2 (Atlas of Plates) in Owen (1879). This depicts the pelvis from 'Cowes' on the Obelisk Range (Now BMNH 75.12.15.34 "33").

DESCRIPTION OF THE PLATES.

PLATE CV.

Figs. 1–4. Pelvis of *Harpagornis moorei*. Figs. 5–7. Pelvis of *Circus pygargus*.

Fig. 6.1H Plate CVI, from Vol. 2 (Atlas of Plates) in Owen (1879).

PLATE CVI.

Figs. 1–6. Humerus of *Harpagornis moorei*.
Figs. 7–12. Humerus of *Circus pygargus*.

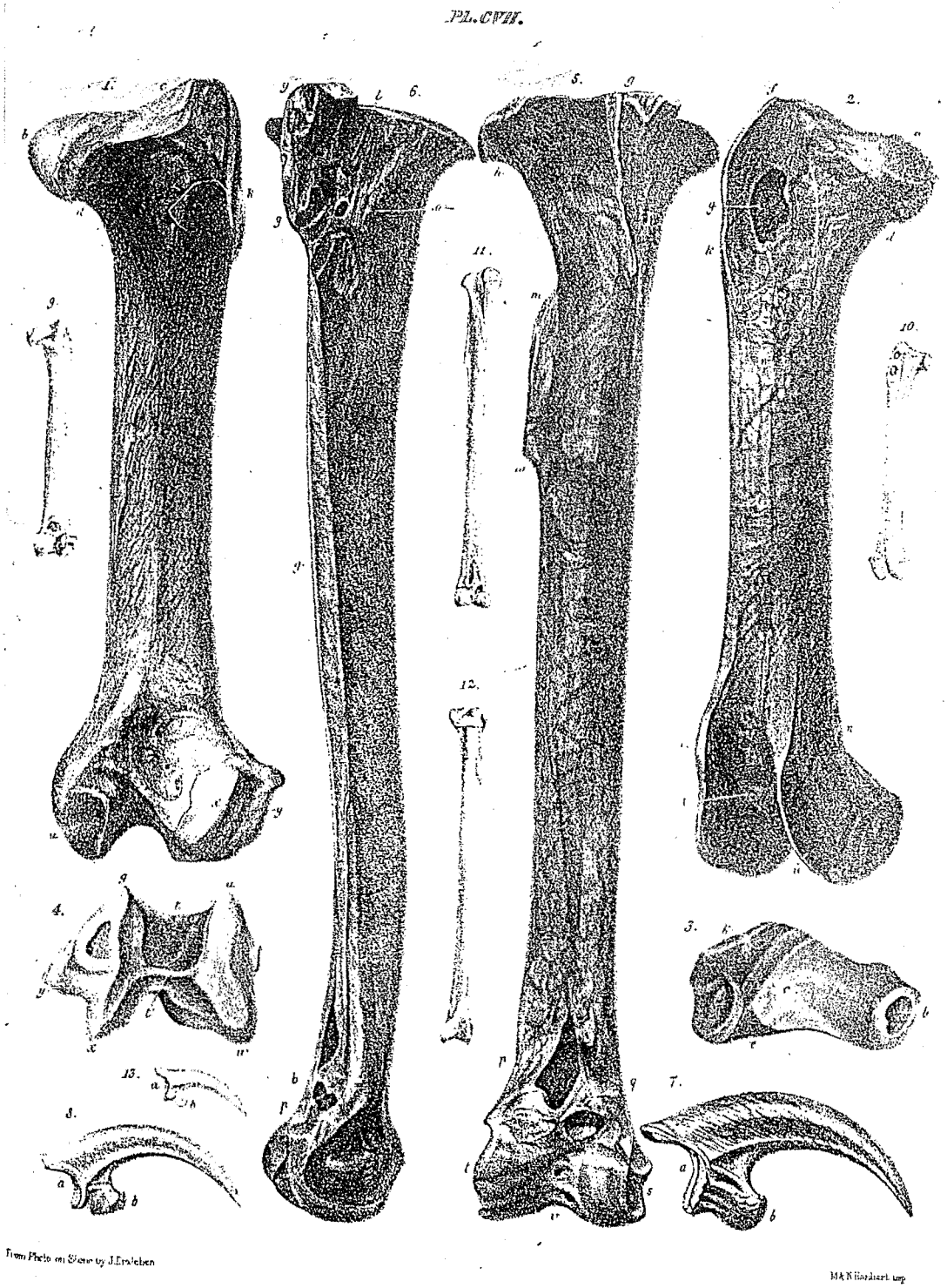


Fig. 6.1I Plate CVII, from Vol. 2 (Atlas of Plates) in Owen (1879).

PLATE CVII.

Figs. 1–4. Femur of *Harpagornis moorei*. Figs. 5, 6. Tibia of *Harpagornis moorei*.
Fig. 7. Side view of ungual phalanx of back toe (*i*) of *Harpagornis moorei*.
Fig. 8. Side view of ungual phalanx of *Aquila cuneicaudata*.
Figs. 9, 10. Femur of *Circus pygargus*. Figs. 11, 12. Tibia of *Circus pygargus*.
Fig. 13. Phalanx of back toe of *Circus gouldi*.

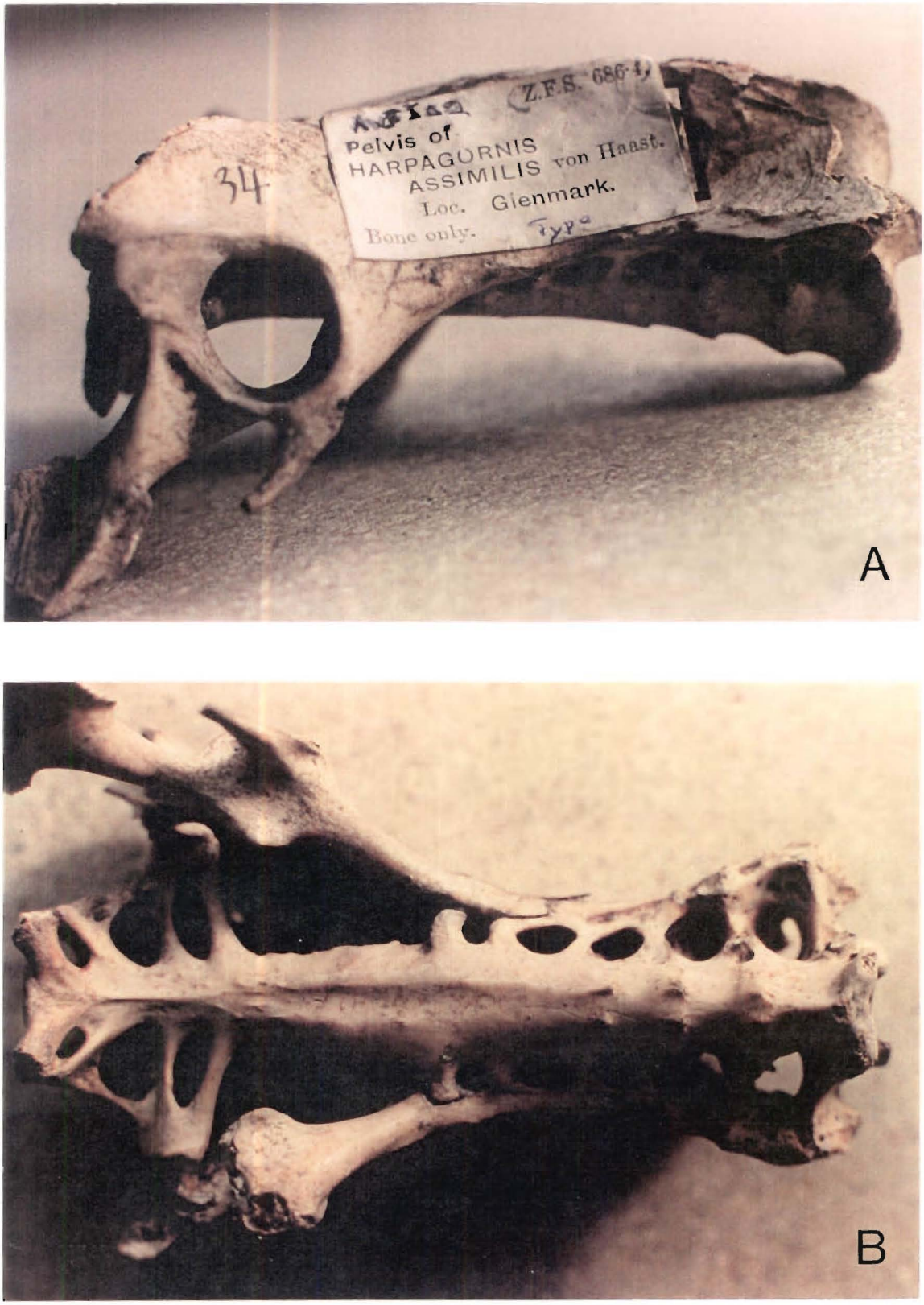


Fig. 6.2 (A, B) Pelvis from type series of *Harpagornis assimilis* Haast, 1874: CMNZ AV 5102pt; in **A**, lateral, and **B**, ventral views.

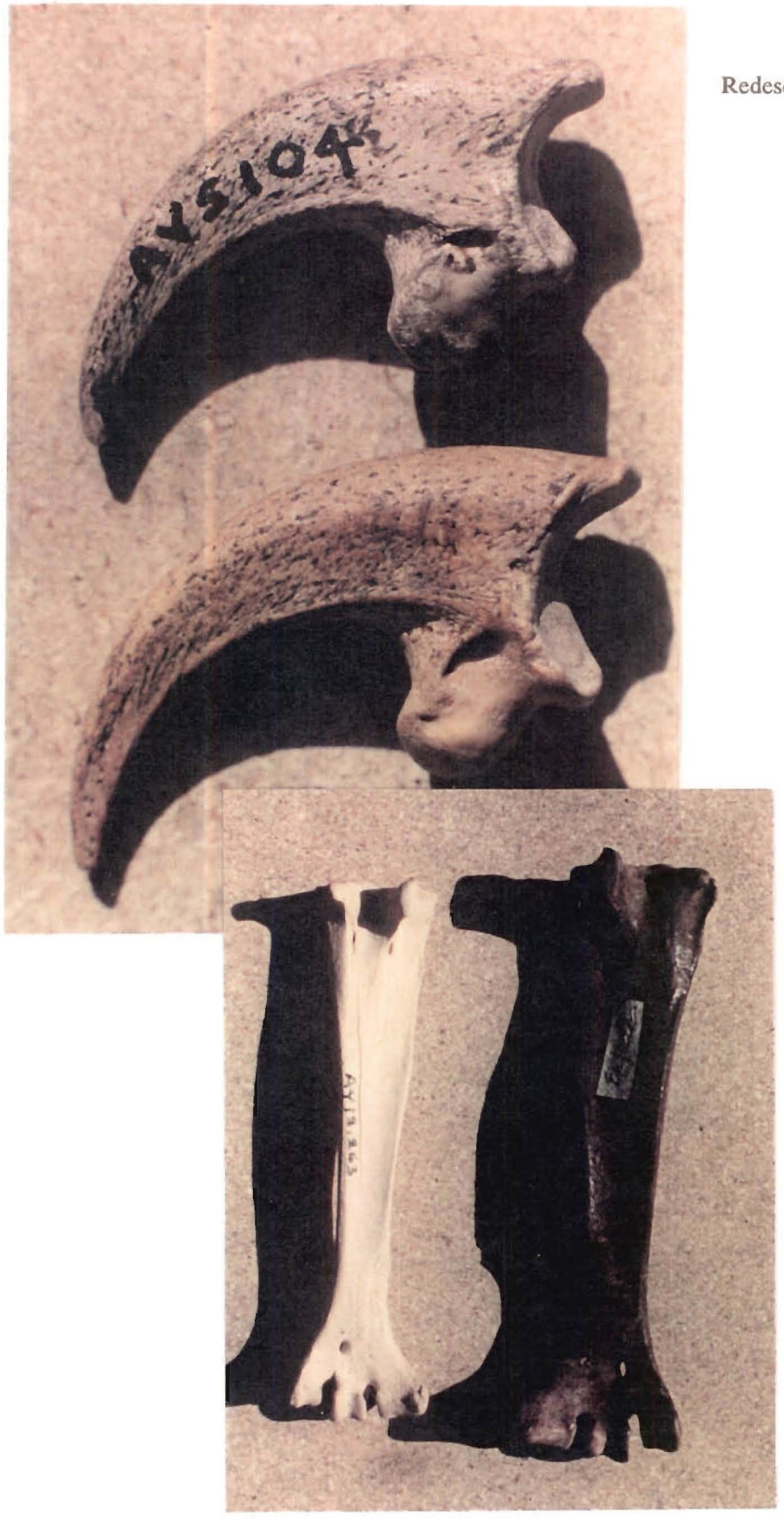


Fig. 6.3 (Top) Ungual phalanges from type individual of *Harpagornis moorei* Haast, 1872, CMNZ AV 5104pt; right lateral view.

Fig. 6.4 (Bottom) Tarsometatarsi of *Harpagornis moorei*; plantar aspects showing effects of exposure to swamp (CMNZ AV 5329; Enfield, dark stained bone) and dune (CMNZ AV 12263; Marfells Beach, pale) sediments.

PLATES

1-16

Plate 1 (A-F) *Harpagornis moorei* Haast, 1872, **lectotype** left femur (CM AV 5104pt), Holocene, Glenmark, F Fuller, Mar 1871: **A**, medial aspect; **B**, cranial; **C**, lateral; **D**, caudal; **E**, proximal; **F**, distal. Scale bar = 10 mm.

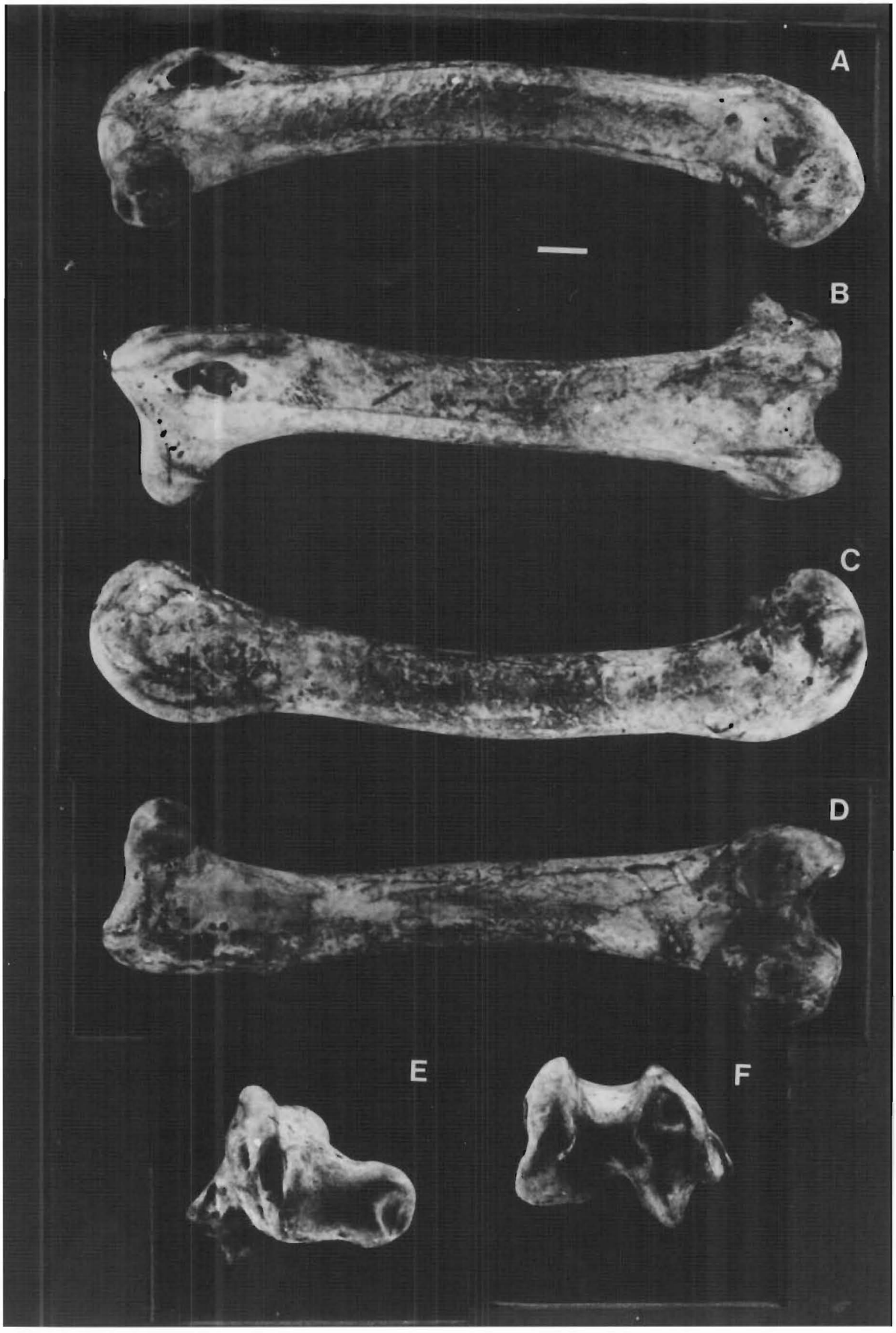

A
B
C
D
E
F

Plate 2 (A-F) *Harpagornis moorei* Haast, 1872. **A-D, lectotype** right femur (CM AV 5102pt) of *Harpagornis assimilis* Haast, 1874, Holocene, Glenmark, Canterbury Museum party, 1872: **A**, lateral; **B**, cranial; **C**, medial; **D**, caudal. **E-F**, left femur (AU 9723pt), Cape Wanbrow (Shirley Creek), Oturian Interglacial, J Grant-Mackie & P R Millener: **E**, cranial; **F**, caudal. These elements presented here for comparison with the ***lectotype*** of *Harpagornis moorei* (Plate 1), to show first that the nominal taxon *Harpagornis assimilis* is identical morphologically to *H. moorei*, and to show that elements from different time horizons are also closely similar in morphology. This further establishes the unitary nature of *Harpagornis moorei*, and its occurrence from at least the Oturian Interglacial until the late Holocene. Scale bar = 10 mm.

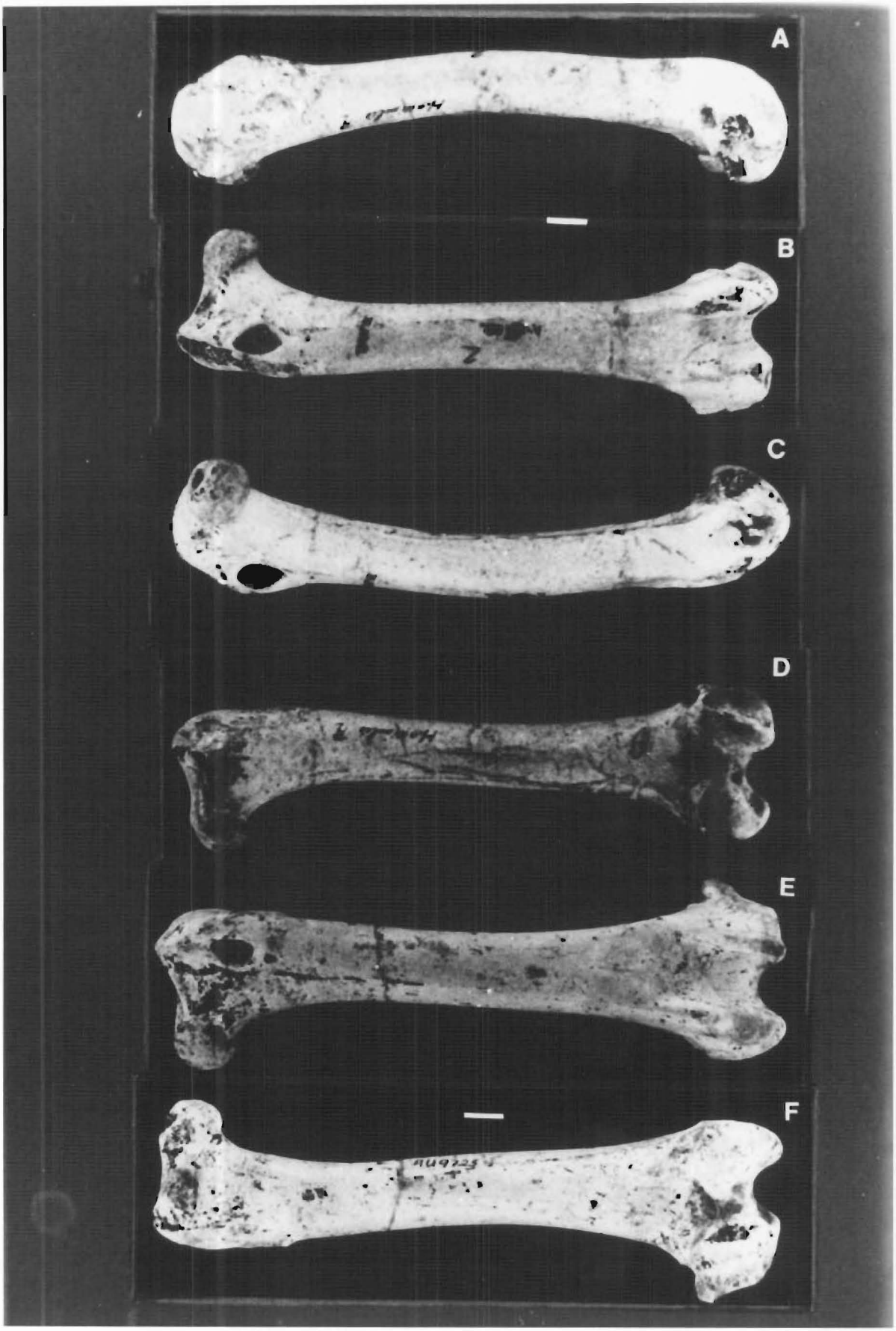

A
B
C
D
E
F

Plate 3 (A-I) Cranium, prefrontal, premaxilla, palate, basicranium, and posteropterygoid: **A-C**, cranium: **A**, dorsal; **B**, left lateral; **C**, ventral, showing palatines, maxillopalatines, and right quadratojugal. **E-I**, posteropterygoid, S 23611 pt, AR 144: **E**, ventral; **F**, dorsal; **G**, medial; **H**, proximal; **I**, distal. **Inset:** Enlargement of basicranium, showing heavy ridges across basisphenoidal plate, and deep fossa anterior to occipital condyle. Note scroll of bone surrounding external naral opening. Scale bars: for **A-C** = 100 mm; for **E-H** = 5 mm.

A
B
C
E
H
F
I
G

Plate 4 (A-E) **A-C** Complete cranium, re-articulated, including full palate, both prefrontals, and both superciliaries, S 27773pt, Mount Owen, Holocene, D Smith T H Worthy P R Millener, Jan 1990; 3 scleral ossicles not shown: **A**, right lateral; **B**, ventral; **C**, dorsal. **D-E**, cranium, AV 5685, Pyramid Valley, 1949: **D**, posterior; **E**, anterior. Scale bar = 100 mm.

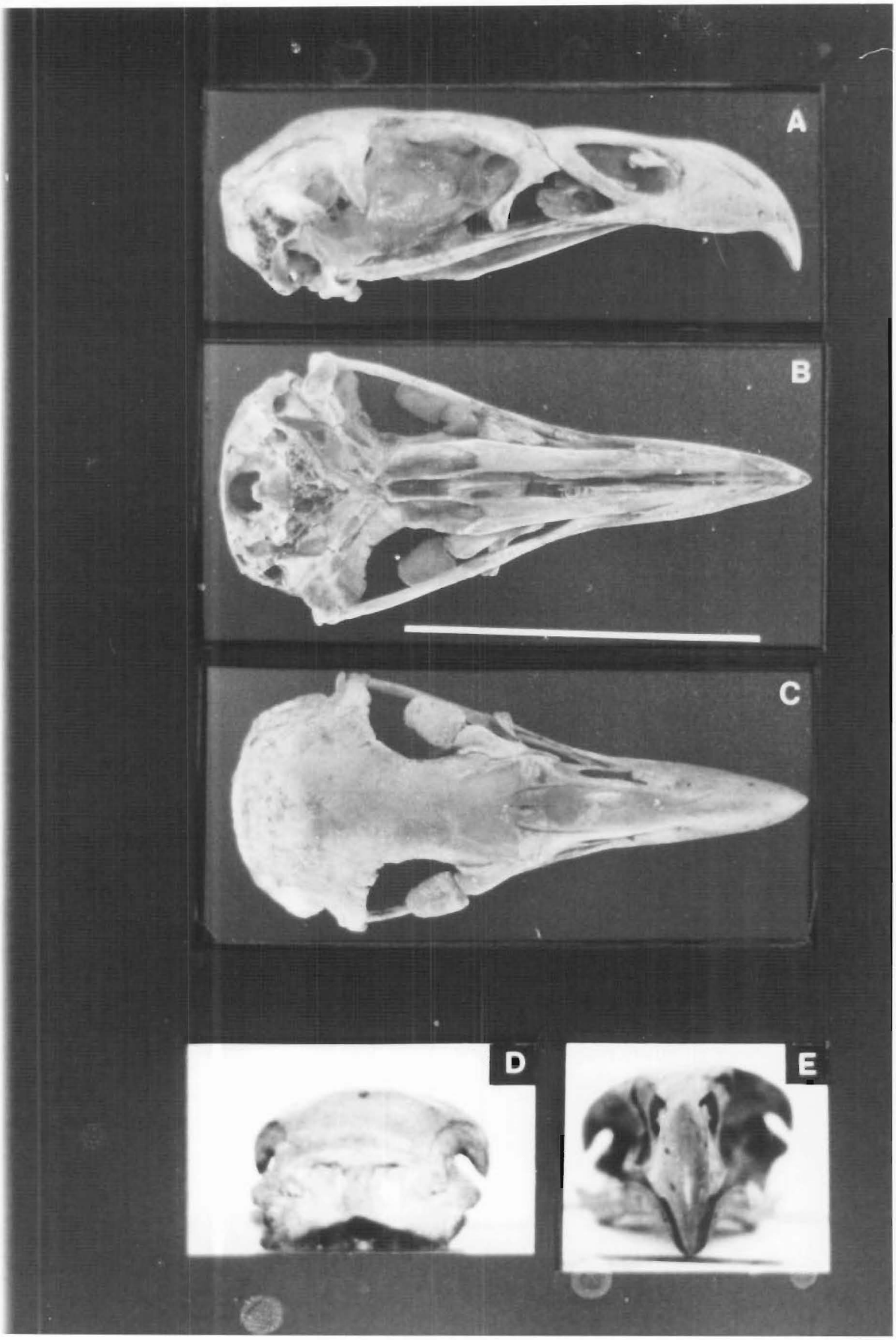

A
B
C
D
E

Plate 5 (A-F) Atlas and axis (cervical 1 and 2) vertebrae, S 27773pt, Mount Owen, D Smith T H Worthy P R Millener, Jan 1990. **A-C**, axis: **A**, right lateral; **B**, cranial; **C**, caudal. **D-F**, axis: **D**, right lateral; **E**, cranial; **F**, caudal. Scale bar = 5 mm.

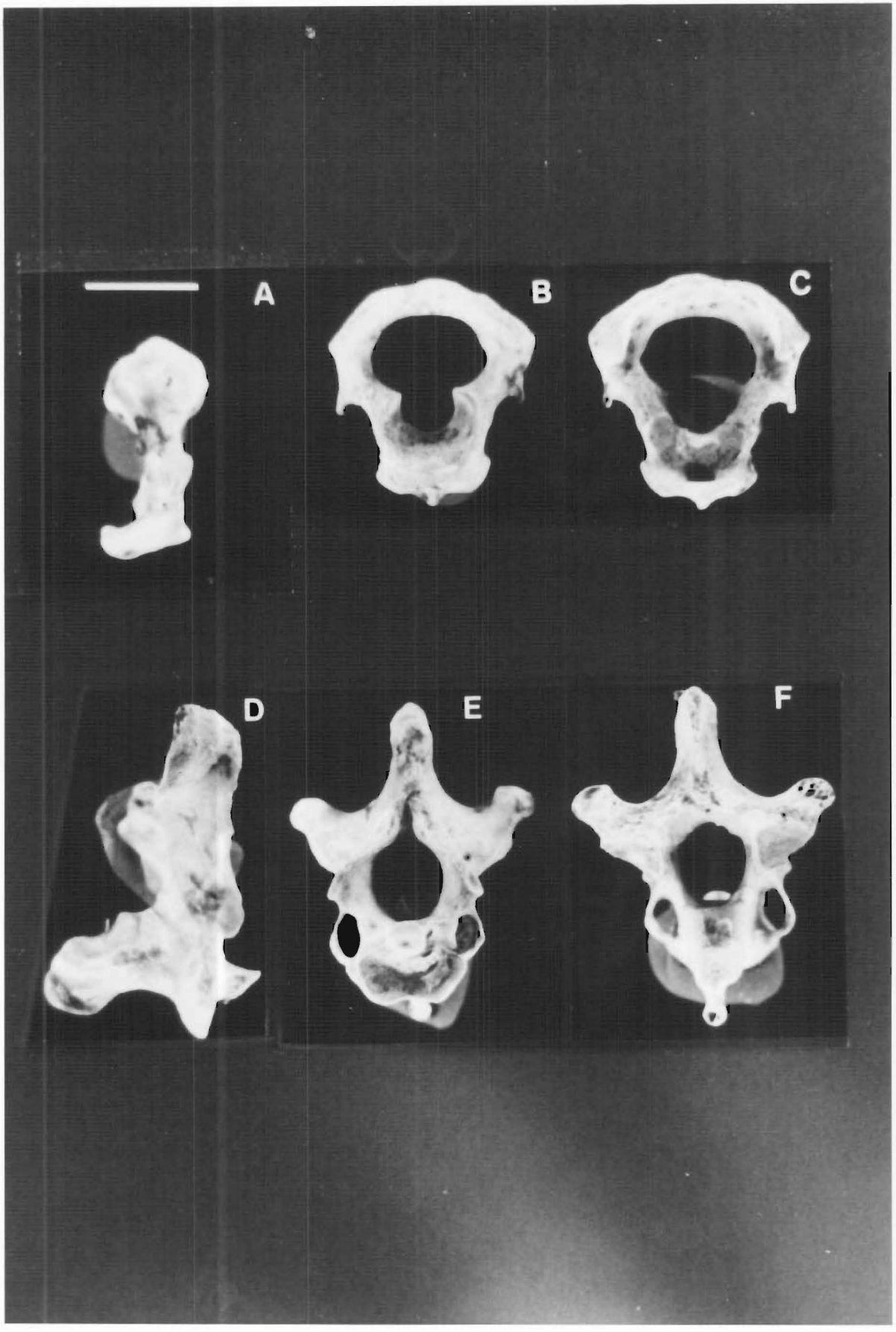

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Plate 6 (A-J) Mandible, hyobranchial apparatus, quadrate. **A-C**, mandible, S 23611, AR 144: **A**, dorsal; **B**, left lateral; **C**, ventral. **D**, hyobranchial apparatus, ventral. **E-J**, right quadrate, DM 2134pt, Castle Rocks: **E**, anterior, optic process to left; **F**, posterior, otic process to right; **G**, dorsal; **H**, ventral; **I**, lateral; **J**, medial. Scale bars: for **A-C** = 10 mm; for **D** = 5 mm; for **E-J** = 5 mm.

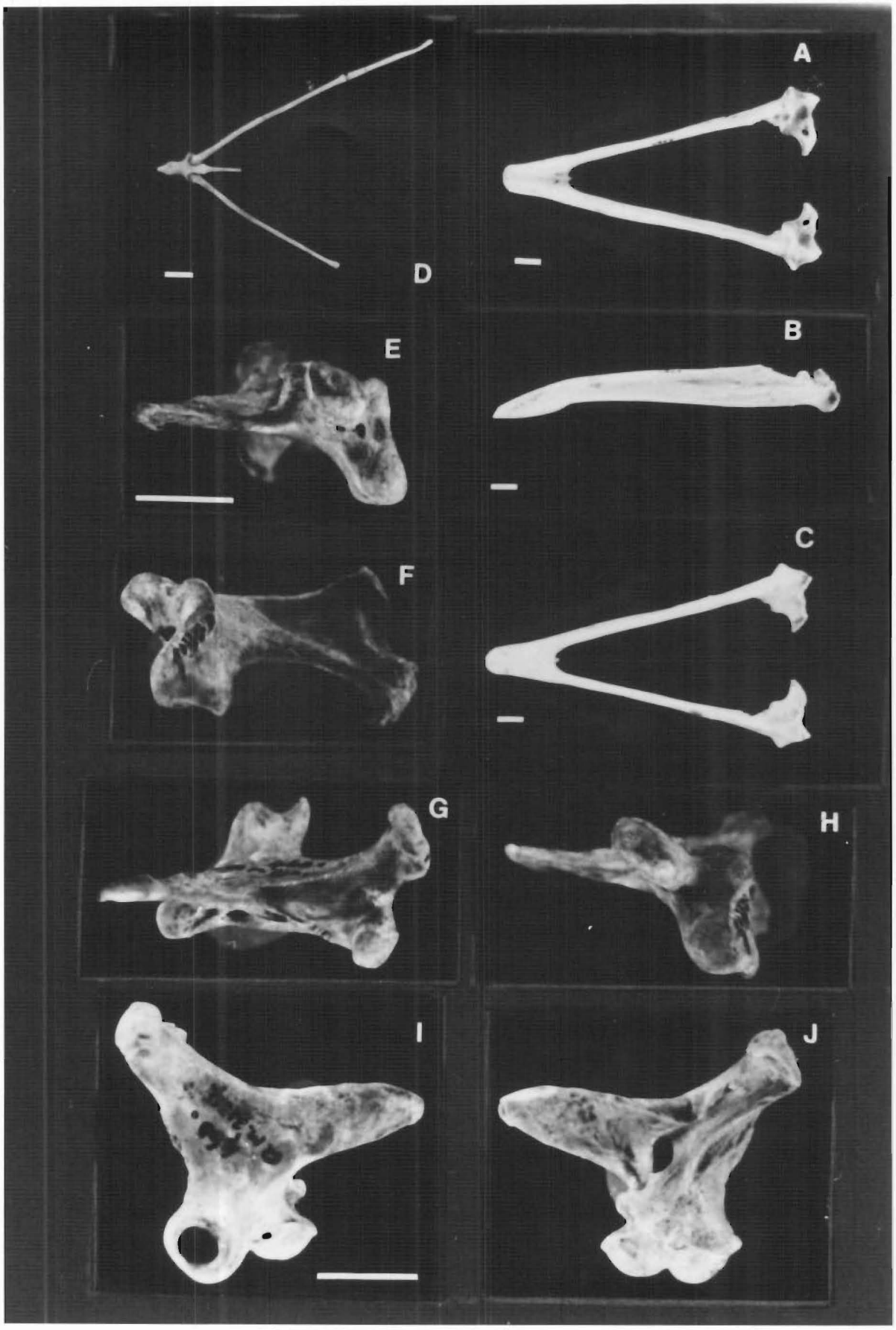
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Plate 7 (A-D) Cervical vertebrae, S 27773pt, Mount Owen, D Smith T H Worthy P R Millener, Jan 1990: **A**, dorsal: **B**, right lateral; **C**, ventral; **D**, cranial. In all, **a-k** are cervicals 1-11 in sequence. Scale bars = 5 mm.

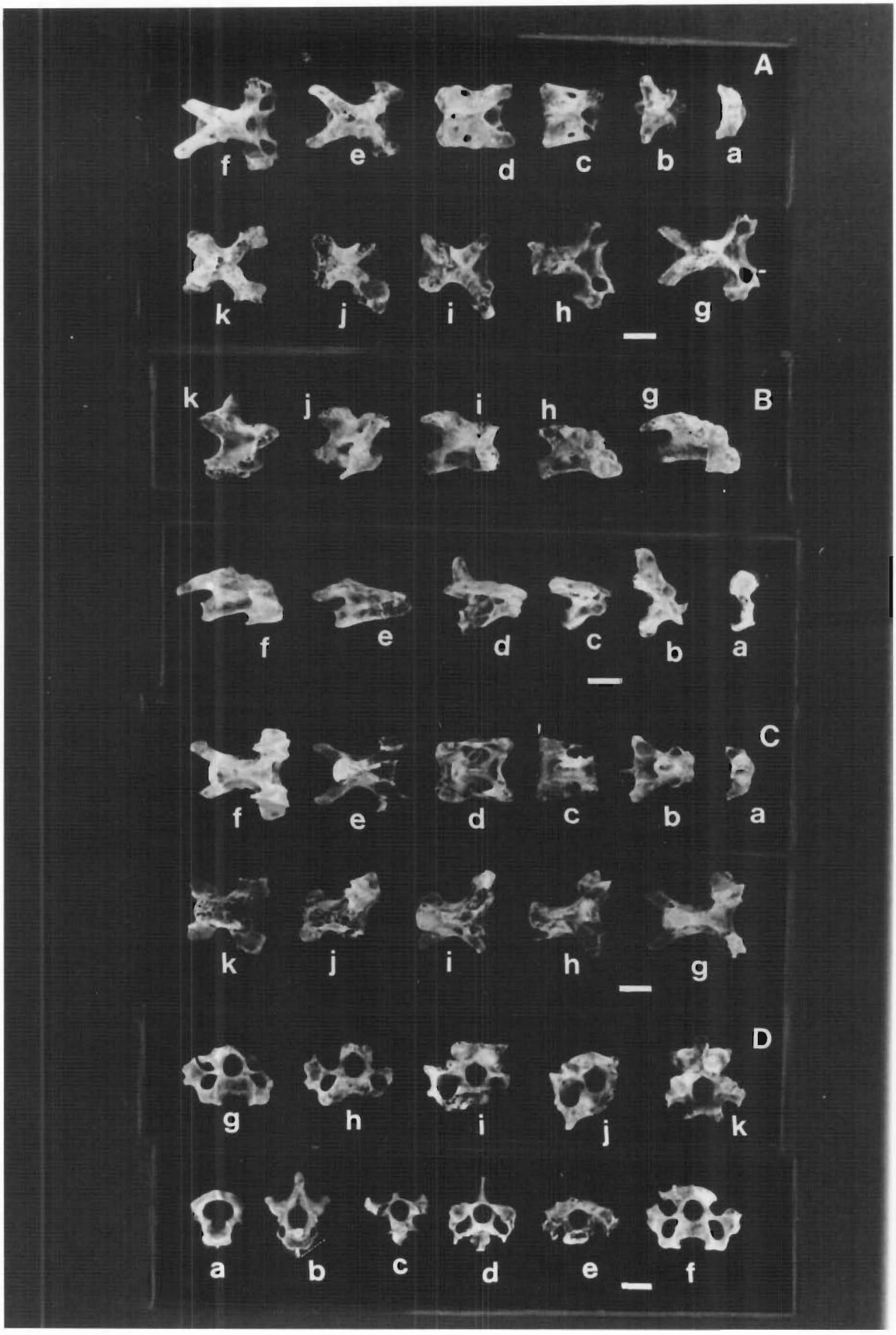
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Plate 8 (A-C) Thoracic (dorsal) and lower cervical vertebrae, S 27773pt, Mount Owen, D Smith T H Worthy P R Millener, Jan 1990: **A**, dorsal; **B**, right lateral; **C**, cranial. In all, **a-h** are cervicals 12 and 13 and thoracics 1-6, in sequence. Scale bars = 5 mm.

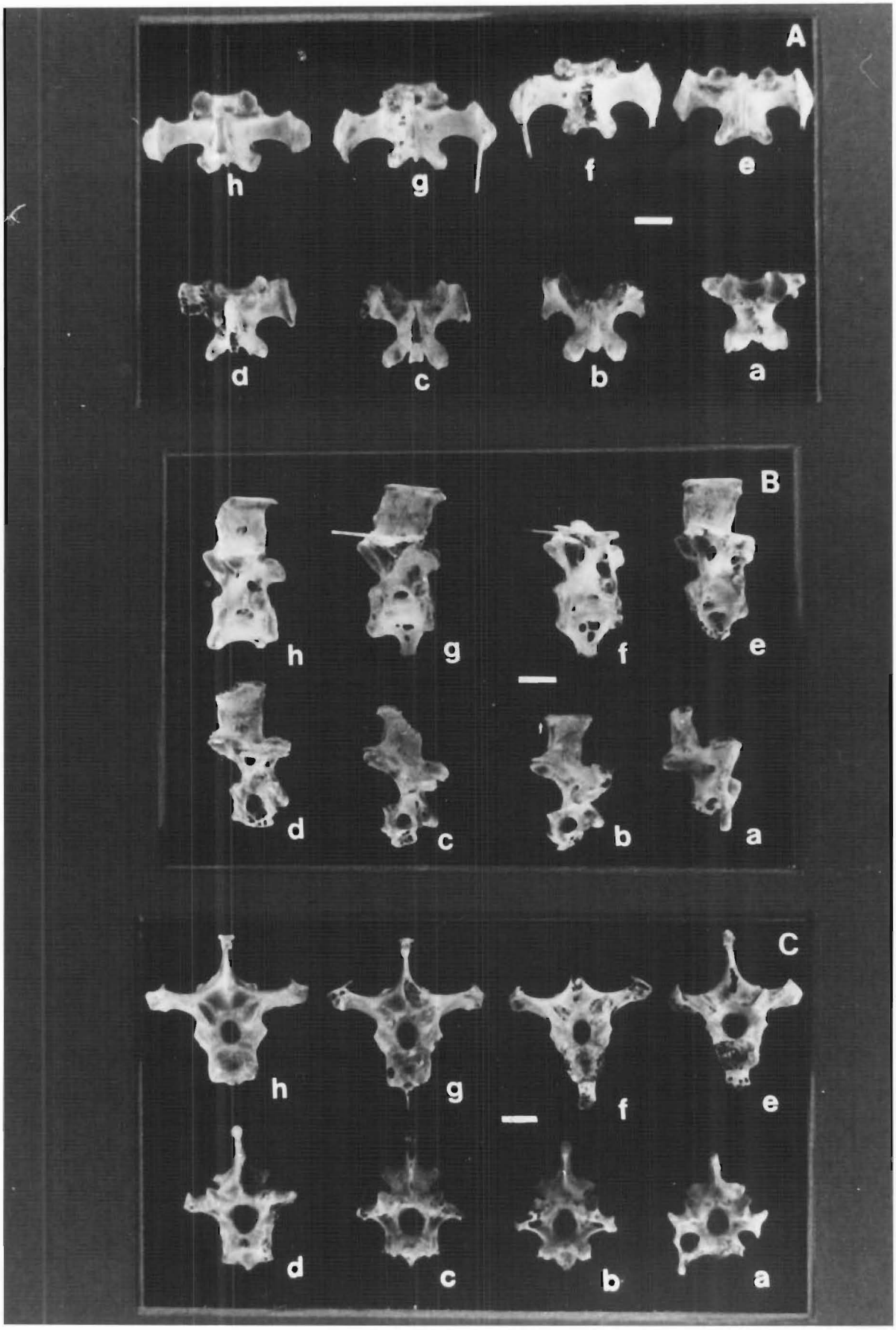
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Plate 9 (A-D) Caudal vertebrae and pygostyle, S 27773, Mount Owen , Jan 1990. **A**, right lateral; **B**, ventral; **C**, caudal; **D**, cranial. In all, **a-f**, caudals 1-6; **g**, pygostyle. Scale bars = 5 mm.

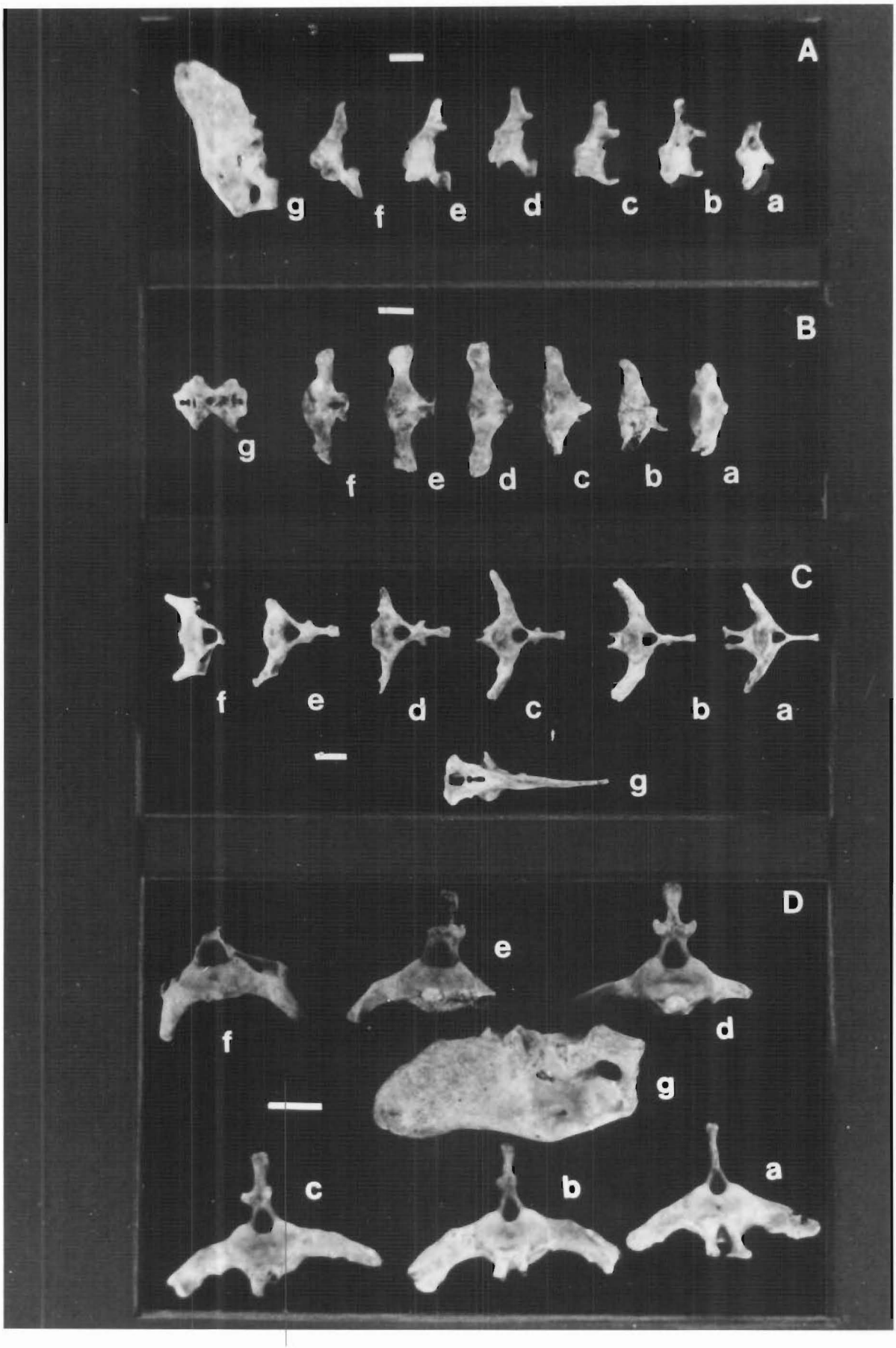
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Plate 10 (A-E) Sternum and pelvis. **A, B,** Sternum, DM 2134pt, Castle Rocks, A Hamilton, 1891: **A,** right lateral; **B,** ventral. **C-E,** Pelvis, DM 2134pt, Castle Rocks, A Hamilton, 1891: **C,** dorsal; **D,** left lateral; **E,** ventral. Scale bar = 100 mm.

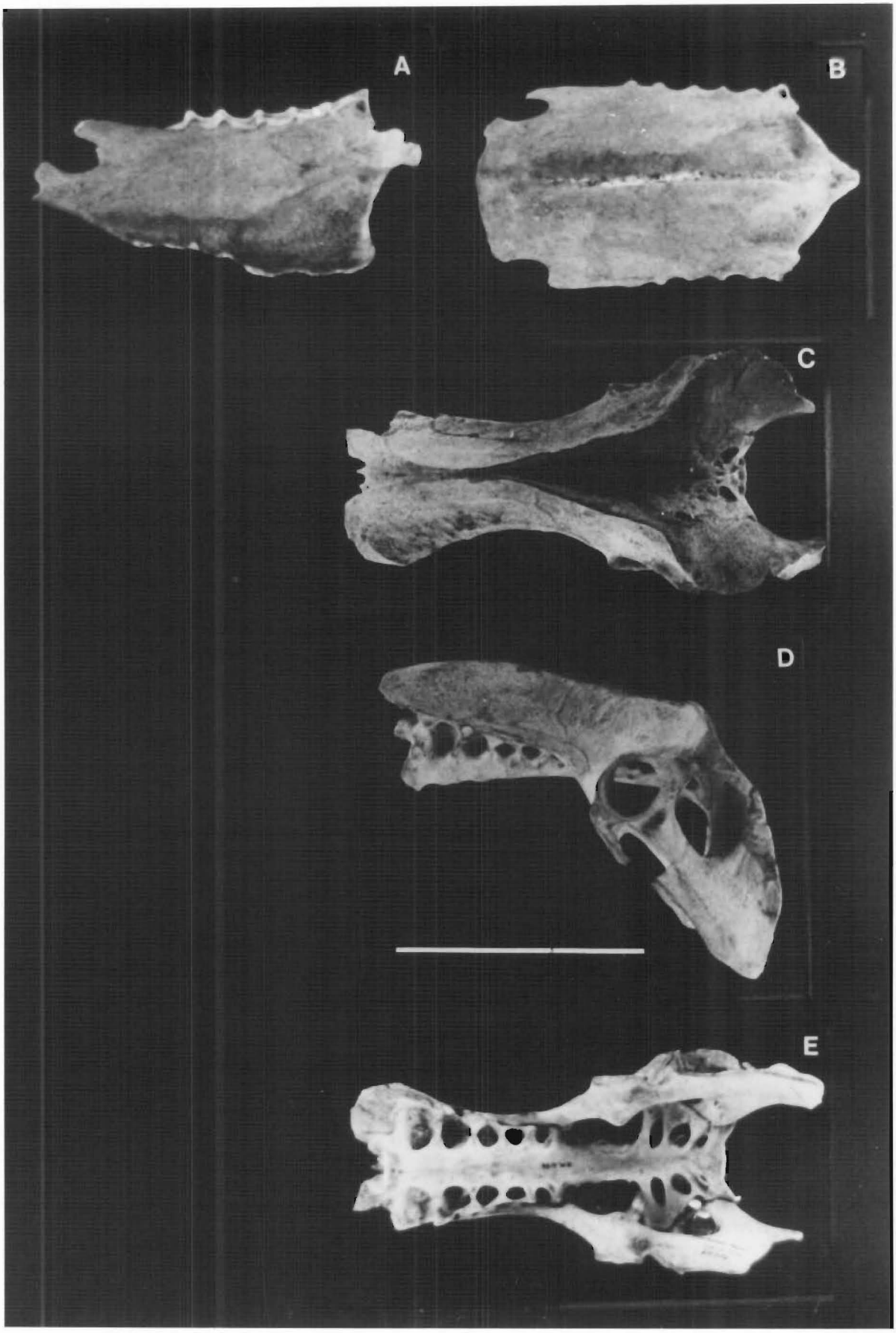
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Plate 11 (A-H) Scapula, coracoid, furcula, humerus. **A, B,** Left scapula, DM 2134, Castle Rocks, A Hamilton, 1891: **A**, lateral; **B**, medial. **C, D,** Right coracoid, S 27773, Mount Owen, D Smith T H Worthy P R Millener, Jan 1990: **C**, ventral; **D**, dorsal. **E, F,** furcula, S 27773, Mount Owen, D Smith T H Worthy P R Millener, Jan 1990: **E**, caudal; **F**, left lateral. **G, H,** Left humerus, S 27773, Mount Owen, D Smith T H Worthy P R Millener, Jan 1990: **G**, anconal; **H**, palmar. Scale bars for: **A-F** = 10 mm; for **G, H** = 100 mm.

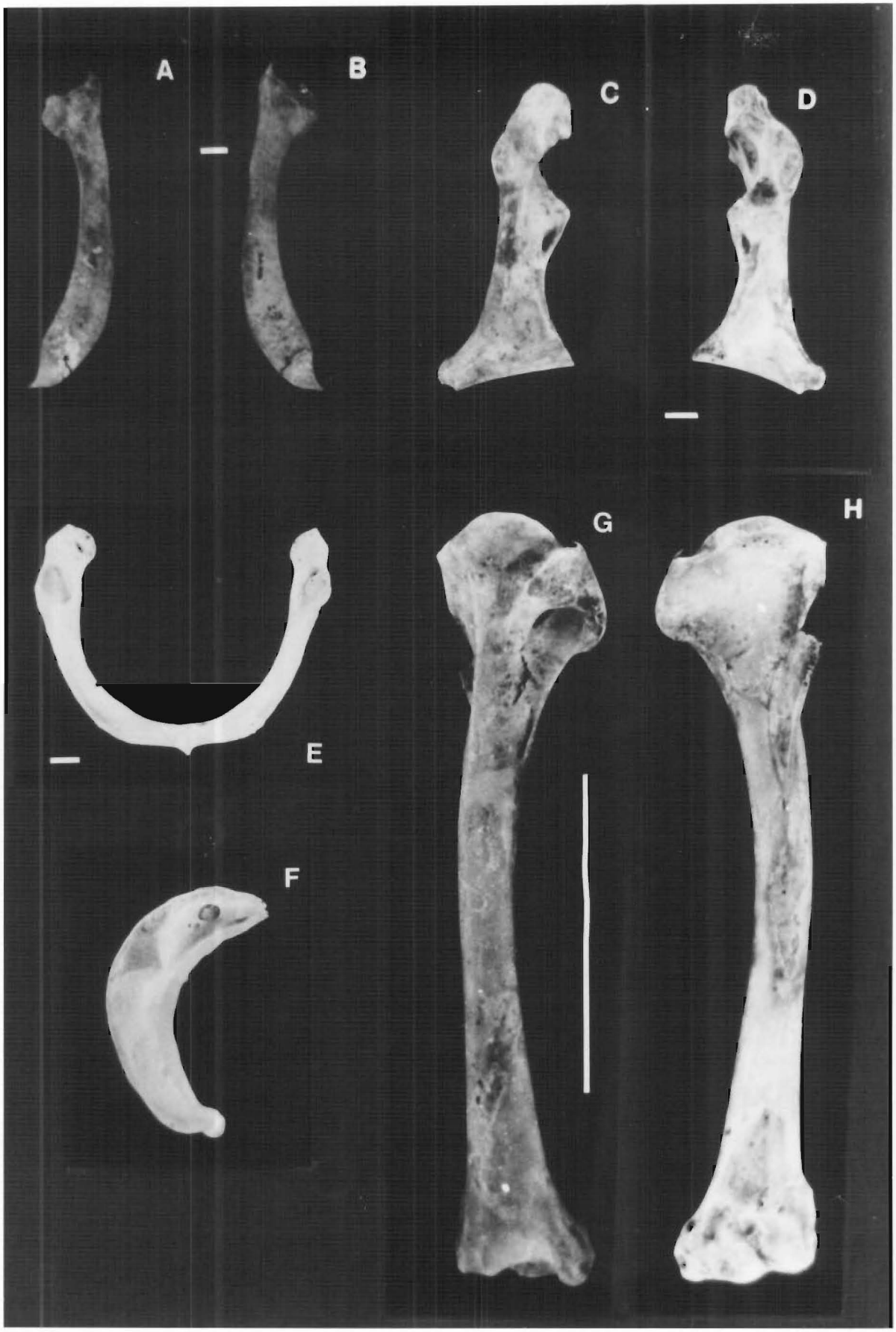
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Plate 12 (A-O) Ulna, radius, carpometacarpus, ulnare, radiale, digit 1 phalanx 1, digit 2 phalanges 1 and 2, digit 3 phalanx 1; all S 27773, Mount Owen, D Smith T H Worthy P R Millener, Jan 1990. **A, B,** right ulna: **A,** palmar; **B,** anconal. **C, D** right radius: **C,** palmar; **D,** anconal. **E, F,** left carpometacarpus: **E,** anconal; **F,** palmar; **G, H,** ulnare. **I, J,** radiale. **K, L,** digit 2 phalanx 1: **K,** left, palmar; **L,** right, anconal. **M,** digit 2 phalanx 2. **N,** digit 3 phalanx 1; **O,** digit 1 phalanx. Scale bars for: **A-D** = 100 mm; for **E, F** = 10 mm; for **H-O** = 10 mm.

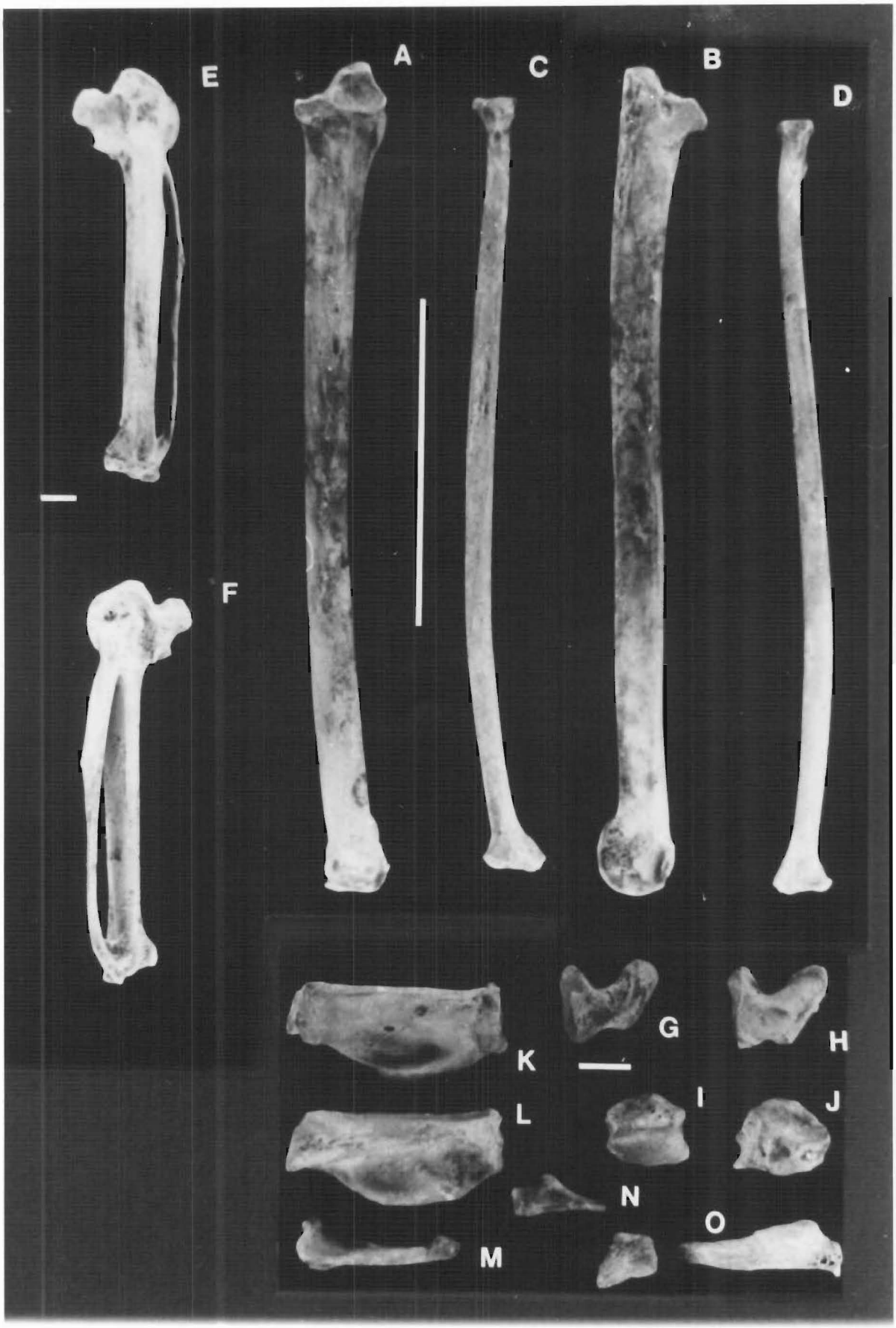
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Plate 13 (A-F) Femur, tarsometatarsus. **A-D**, Left femur, S 27773, Mount Owen, D Smith T H Worthy P R Millener, Jan 1990: **A**, lateral; **B**, cranial; **C**, medial; **D**, caudal. This element is important in that its morphological identity with both **lectotypes**, and with older material, allows the undoubted associated material of this almost complete skeleton to be used as identification masters. **E, F**, left tarsometatarsus: **E**, cranial; **F**, caudal. Scale bar = 100 mm.

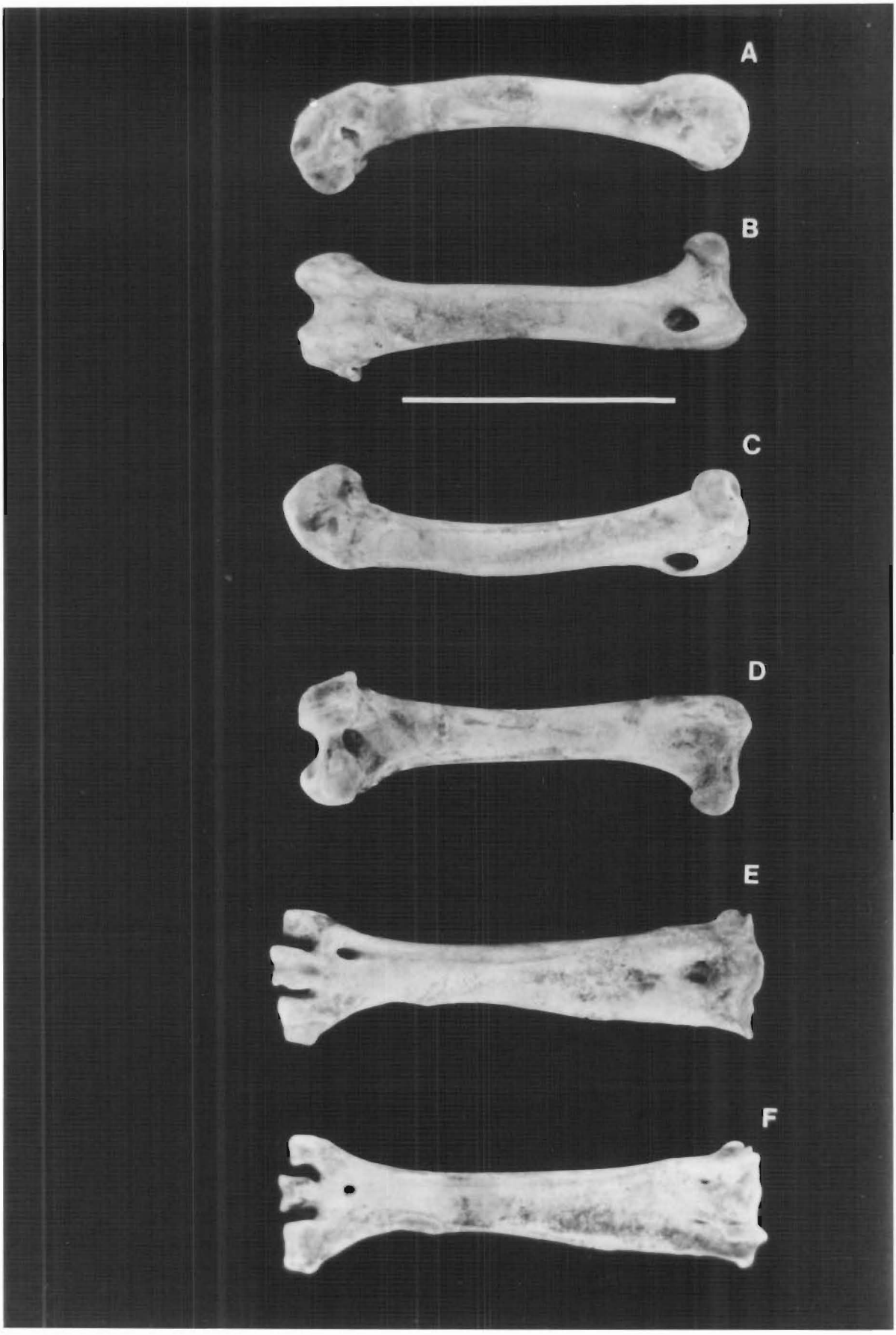
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Plate 14 (A-D) Tibiotarsus and tarsometatarsus. **A, B,** right tarsometatarsus, S 27773, Mount Owen, D Smith T H Worthy P R Millener, Jan 1990: **A,** cranial; **B,** caudal. **C, D,** Left tibiotarsus, S 27773, Mount Owen, D Smith T H Worthy P R Millener, Jan 1990: **C,** cranial; **D,** caudal. Scale bars = 100 mm.

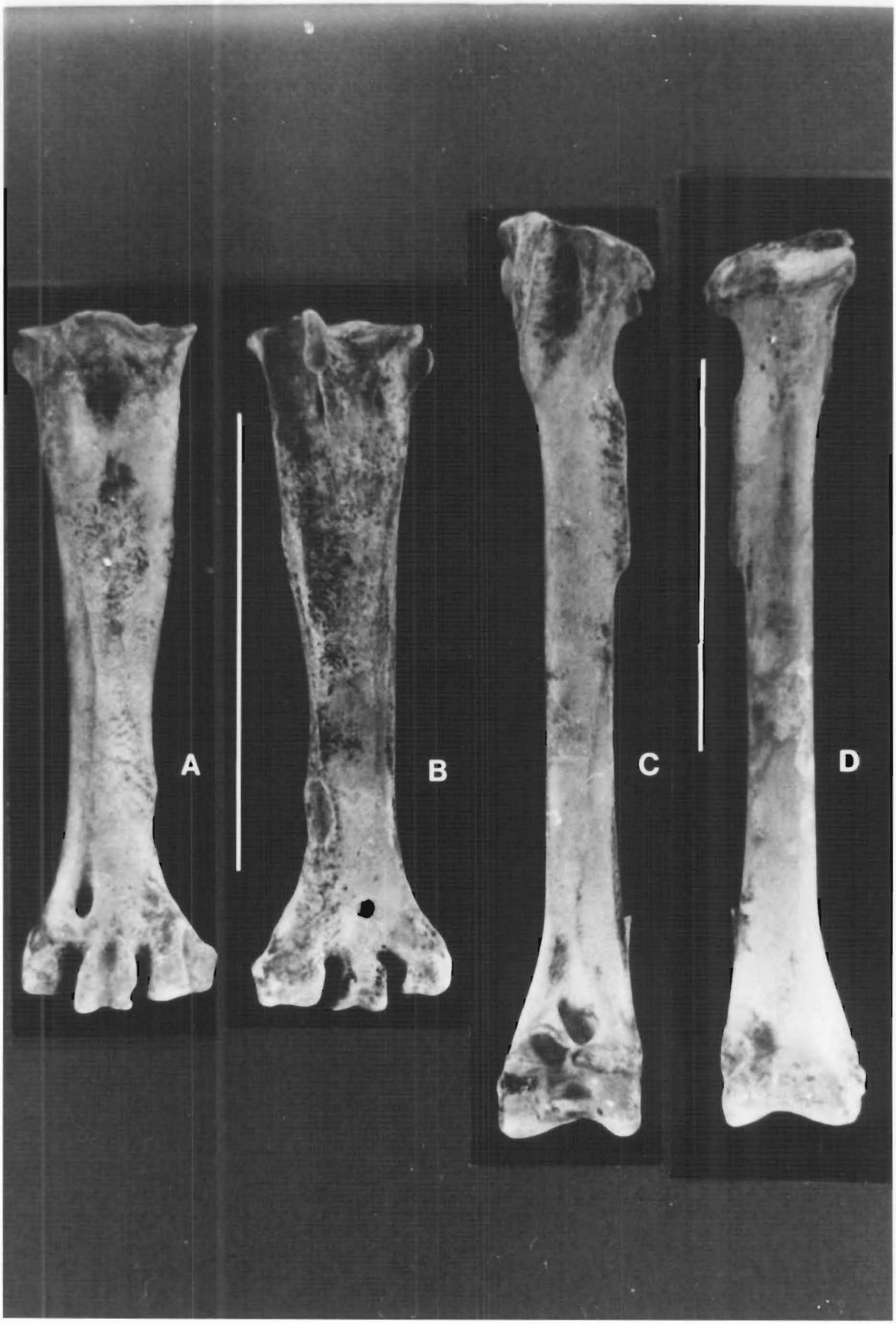
A
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Plate 15 (A-C) First metatarsal and pedal phalanges, right pes. **A-C**, first (hind) digit: **A**, first phalanx; **B**, second (ungual) phalanx; **C**, first metatarsal. **D-F**, second digit: **D**, first phalanx; **E**, second phalanx; **F**, third (ungual) phalanx. **G-J**, third digit: **G**, first phalanx; **H**, second phalanx; **I**, third phalanx; **J**, fourth (ungual) phalanx. **K-O**, fourth digit: **K**, first phalanx; **L**, second phalanx; **M**, third phalanx; **N**, fourth phalanx; **O**, fifth (ungual) phalanx. All cranial views, except ungual phalanges, which are right lateral. All elements 5/6 full size.

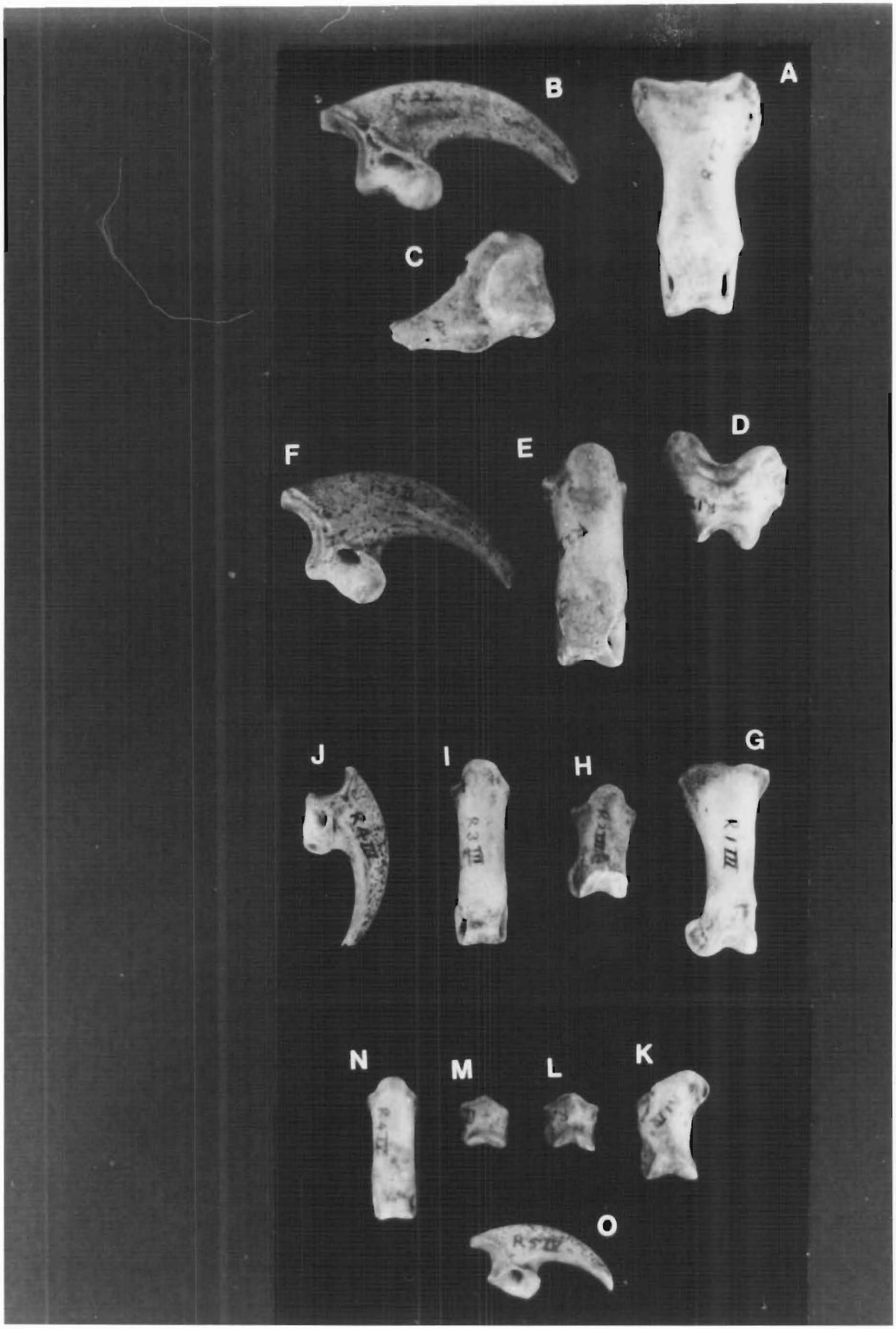
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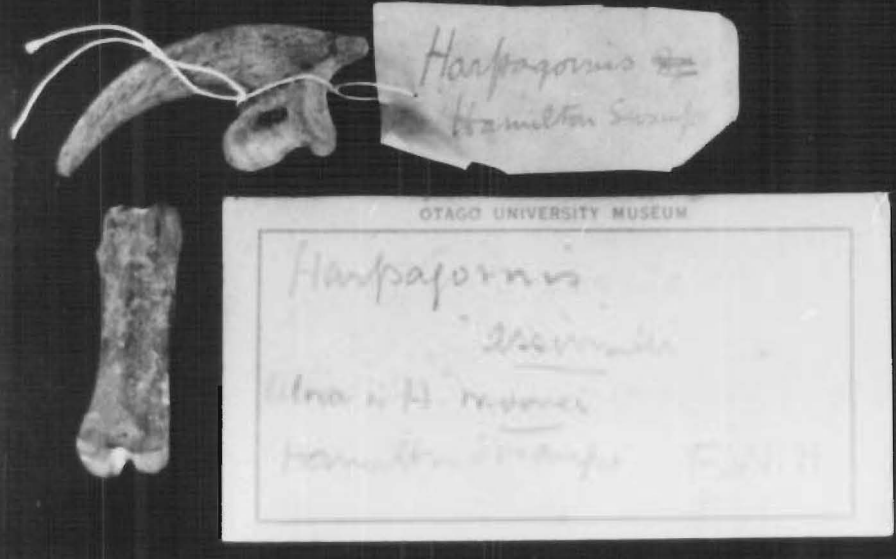
Plate 16 (A, B) **A**, First bone of *Harpagornis moorei* to enter a collection, the right digit two, phalanx one from Waingongoro, collected by W Mantell in 1847 and sold to the British Museum (BMNH 32245h). The pale, leached nature of the bone suggests that it is dune, not swamp, material, which supports its origin from Waingongoro and not Waikouaiti, where Mantell also collected. **B**, Two pedal phalanges from Hamilton Swamp, with labels in Hutton's hand.

A

B



Ungual 49.3 26.7 18.4 10.0 Probably II/3
Pedal 37.4 Probably III/3 H Hum Hen

CHAPTER 2A

HARPAGORNIS ASSIMILIS HAAST, 1874, A SYNONYM OF *HARPAGORNIS MOOREI* HAAST, 1872 (AVES: ACCIPITRIDAE)

R.N. HOLDAWAY

Department of Zoology, University of Canterbury, Christchurch 1, New Zealand.

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ABSTRACT

Holdaway, R.N. (1990). *Harpagornis assimilis* Haast, 1874, a synonym of *Harpagornis moorei* Haast, 1872 (Aves: Accipitridae). *New Zealand Natural Sciences* 17: 39-47.

The taxonomic status of *Harpagornis assimilis* Haast, 1874 (Aves: Accipitridae) is discussed in relation to the characters supposedly separating it from *Harpagornis moorei* Haast, 1872. Length measurements of the pooled sample of specimens from both nominal taxa had a size-independent variability similar to that in the living harpy eagle *Harpia harpyja*, whose bone lengths approach that of the smallest New Zealand material, and which is sexually size dimorphic. This suggests that Harpagornis *assimilis* was based on the smaller sex of a single, sexually size-dimorphic species. *Harpagornis assimilis* is therefore a junior synonym of *H. moorei*.

KEYWORDS: Accipitridae - New Zealand - fossil - taxonomy - *Harpagornis moorei* - morphometrics.

INTRODUCTION

Haast (1874) proposed the name *Harpagornis assimilis* for the smaller of two partial skeletons of eagles found in swamp deposits at Glenmark, North Canterbury, New Zealand. In his description, he stated that it differed from *Harpagornis moorei* Haast, 1872, only in being somewhat smaller. He pointed out that the type specimens of both taxa were from adult birds and that the minor differences in morphology between comparable bones from the two type series were individual differences "of no specific value". Haast was aware that there is often pronounced sexual size dimorphism in accipitrids, and suggested that the smaller bird was just the male of *Harpagornis moorei*. But he had little material, and "as I am not able to settle this point at present, I shall propose for the second and smaller specimen the specific name of *H. assimilis*, in order to point out the close relationship of both". *Harpagornis assimilis* has been accepted or rejected as a valid taxon by various workers since Haast, but none of these has presented evidence in support of their views. Owen (1879) did not mention that the smaller bird had been given a separate name, and he included descriptions and illustrations of both nominal taxa in his memoir. Lydekker (1891) listed *H. assimilis* as a synonym of *H. moorei* but with a query. Hamilton (1893) listed most of the material known at the time, separating that referred to each nominal species. Lambrecht (1933) listed *H. assimilis* as a synonym of *H. moorei*, but then gave dimensions for both, including separate ranges for the humerus, ulna, radius, femur, tibiotarsus, and tarsometatarsus. Oliver (1930, 1955) recognised both species, listing their bone lengths and geographic ranges separately.

Scarlett (1972) gave ranges of dimensions for six elements (femur, tibiotarsus, tarsometatarsus, humerus, ulna, radius) and illustrated these and five others (coracoid, scapula, sternum, carpometacarpus, and ungual phalanx). He noted that "*H. assimilis* [was] a name we now regard as a synonym for *moorei*". The current New Zealand *Checklist* (Kinsky 1970) also states definitely that *H. assimilis* was simply the male of *H. moorei*.

Important avian bone deposits excavated in the Honeycomb Hill series of caves in northwest Nelson include the remains of more than 10 eagles (Millener 1984, Worthy 1987, Worthy & Mildenhall 1989). These and other recent finds

provide sufficient material to allow the taxonomic status of *H. assimilis* to be resolved. Haast's description of *H. assimilis* as a smaller species than *H. moorei* leads to the prediction that the dimensions of eagle bones from New Zealand subfossil sites should fall into two size ranges, with the type series of each species falling within the appropriate range. The size distributions should be mutually exclusive, or at least display much greater variability than that for existing species of large eagle. As most members of the Accipitridae are sexually size dimorphic (Brown & Amadon 1968), it is possible that morphometric differences between two taxa where the female of the smaller species was about the same size as the male of the larger would be largely obscured by the overlap of dimensions. This is unlikely in the present instance because there is no other instance of sympatry between extremely large, closely related accipitrids, and there are no morphological differences between the type material of *H. assimilis* and *H. moorei* (author's unpublished data).

Therefore, Haast's suggestion that there may have been two sympatric species, a suggestion set in taxonomic concrete by his publication of the name *H. assimilis*, cannot be supported if the variability within the pooled sample from both nominal species does not exceed that for a living species of similar size (Cracraft 1976). If the distributions were discrete, but monomodal, it would suggest that two monomorphic species were represented: size monomorphy is highly unusual in the large eagles.

Conversely, Haast's counter proposal that the smaller taxon represents the other sex in a sexually size-dimorphic *H. moorei* can be rejected if the size distributions for the major bones are monomodal.

Practically, *Harpagornis assimilis* cannot be supported if the range, and variability independent of size (measured by the coefficient of variation) for all dimensions of specimens assigned to both nominal taxa are commensurate with those from living species of large accipitrids, and the variability is much less than that between living taxa. The harpy eagle (*Harpia harpyja*) was used for comparison because, although it is not phylogenetically close to the genus *Harpagornis* (author's unpublished data), it is the largest living eagle.

Evidence for broad sympatry of the nominal taxa would also strongly favour rejection of *H. assimilis*.

In this note, I present measurements and basic statistics for the major axial and appendicular bones attributed to both nominal species. The relative geographic distribution of specimens assigned to both nominal species is evaluated. Size distributions for all major elements are described, and the validity of *Harpagornis assimilis* Haast, 1874 is discussed. The evidence for sexual size dimorphism within *H. moorei* is also assessed.

MATERIALS AND METHODS

I measured all major elements of the axial and appendicular skeleton of specimens attributed to both nominal taxa, which were complete enough for meaningful measurement. Measurements were made with vernier calipers, to the nearest 0.1 mm. Many otherwise intact bones were worn on their articular surfaces, so lengths are minimal values in many instances. The length was usually underestimated by less than 2 mm, which is less than 1% for many of the long bones. The magnitude of the discrepancy was insufficient to affect the conclusions reached here.

Material was measured in the collections of Canterbury Museum (CMNZ, Christchurch), National Museum of New Zealand (NMNZ, Wellington), Otago Museum (OMNZ, Dunedin), and the Palaeontology Department, British Museum (Natural History) (BMNH, London). These four collections contain most of the known material. One measurement, the width of a furculum held in the Southland Museum (SMNZ, Invercargill), was not made personally.

Where elements from both sides of an individual from one site were available, the measurement of the left side element was used unless it was too badly worn. Mean lengths of left and right elements for single individuals were not used because only a few individuals were recognisable, and in those the different sides usually differed by less than 1%.

I tabulated basic statistics (mean, standard deviation, range, and coefficient of variation

(CV)) for bone lengths (and width for the furculum), and constructed frequency dot-diagrams of lengths. Frequency histograms were not used because the small sample sizes resulted in marked size-class-dependent effects on the shapes of the distributions. Lengths were considered adequate measures of individual size for this analysis; a detailed analysis of morphometrics will be given elsewhere.

The descriptive statistics and dot diagrams were examined to see if the overall variability was greater than expected for a single taxon, and for evidence of sexual size dimorphism. The range and CV for each element were also compared with data from specimens of *Harpia harpyja*, the extant harpy eagle of Central and South America, in the collections of the British Museum (Natural History), Tring (BMNH), and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (NMNH). A list of specimens used for this study is given in Appendix I.

Site records for each taxon were tabulated, and compared to assess the extent of sympatry. Material collected after 1955 has been referred to *Harpagornis moorei*; the distribution data for this material was not used in this analysis.

RESULTS

The measurements by which Haast differentiated *Harpagornis moorei* and *H. assimilis* (Haast 1874) are given in Table 1, along with my own measurements of his material. Measurements of bones which Haast (1874) attributed to *H. moorei*, but which are not part of the type series, are also given. Hamilton (1893) summarised the collections available in the early 1890s; his measurements (Table 1) demonstrate that some shrinkage occurred during the first years of storage. Such shrinkage is normal in bones recovered from swamps. Although neither Haast nor Hamilton stated explicitly his measurement landmarks, the three sets agree well and observer bias was considered not to be a significant factor in this study.

When Hamilton (1893) remeasured the type material in the Canterbury Museum, (including the second, non-type, series of *H. moorei* from Glenmark) and compared them with Haast's, he miscalculated the conversions from inches to millimetres. For example, he converted Haast's 4.48 inches for the carpometacarpus length to 105 mm, not 113.8 mm. He concluded that Haast's measurements were inaccurate, but his own measurement of 113 mm for that same bone agrees well with Haast's, as does his 155 mm for the *H. assimilis* femur, and the other bones as well.

Table 1. Lengths of major limb bones from the type series of *Harpagornis moorei* Haast, 1872, and *Harpagornis assimilis* Haast, 1874, and from material referred to *Harpagornis moorei* by Haast (1874). Metric equivalents (mm) of original Imperial measurements (inches) in square brackets. + indicates minimal measurement because of wear on bone. - indicates none available.

Element and authority	Nominal taxon	
	H. moorei	*H. assimilis*
Femur		
Haast	169.2 (6.66)	154.7 (6.09)
Hamilton[1]	(166)[2]	155
Present	166.9	153.3, 154.5
Tibiotarsus		
Haast	241.8 (9.52)	226.6 (8.92)
Hamilton	236, 239	227
Present	239.8+, 242.1	219+, 219+
Tarsometatarsus		
Haast	154.4 (6.08)	149.1 (5.87)
Hamilton	155	148
Present	154.8, 153.6	147.6, 147.7
Humerus		
Haast	-	217.7 (8.57)
Hamilton		216
Present		216.4
Ulna		
Haast	255.5 (10.06)	237.5 (9.35)
Hamilton	250, 250	232, 235
Present	254.4+	231.2, 236.1
Carpometacarpus		
Haast		113.8 (4.48)
Hamilton		113
Present		113.1+

[1] Hamilton (1893).

[2] not measured by Hamilton but quoted by him as conversion from Haast's (Imperial) measurement.

Summary statistics for the lengths of princi-

pal bones referred to both nominal species are given in Table 2, and for four skeletons of *Harpia harpyja* in Table 3. The coefficients of variation (size-independent measures of variation, Sokal & Rohlf 1979) for *Harpagornis* were less than, or equal to, those for *Harpia harpyja*. The mean CV for *Harpagornis* was 6.72% (range 4.14-10.71%), just over one-third of that for all bone dimensions in a between-species analysis of 13 species of large accipitrids (17.63%, range 9.27-26.84%; author's unpub. data). Therefore, the size-independent variation in the lengths of the main bones in the pooled samples of the nominal taxa *H. moorei* and *H. assimilis* was about the same as that in a living species of sexually size-dimorphic accipitrids and far less than that expected between species in the Accipitridae. The variability values indicate that only one species was represented in the sample.

This was confirmed by inspection of the frequency dot-diagrams of size distribution for the various bones (Fig. 1). Measurements of the type series specimens of both taxa, and of the material that Haast (1874) referred to *H. moorei*, fell well within the limits of the range for the whole sample.

Table 2. Measurements (mm) and descriptive statistics for the lengths (width for furculum) of the principal axial and appendicular bones of skeleton of *Harpagornis moorei* Haast, 1872 and *Harpagornis assimilis* Haast, 1874.

Element	Mean	Range	SD	SE_x	CV	*n*
Non-paired elements						
Cranium + premaxilla	159.63	151.2-166.9	6.61	2.204	4.14	9
Mandible	122.68	116.0-130.8	5.55	1.961	4.52	8
Furculum	101.85	95.3-110.0	6.73	2.749	6.61	6
Sternum	153.22	140.3-167.2	12.48	5.583	8.15	5
Pelvis	177.26	157.0-197.5	14.92	5.641	8.42	7
Paired elements						
Scapula	127.48	116.7-142.3	9.39	3.831	7.36	6
Coracoid	94.10	78.1-106.6	10.08	3.187	10.71	10
Humerus	230.58	208.0-256.0	14.51	3.520	6.29	17
Ulna	254.48	228.1-281.5	16.51	3.892	6.49	18
Radius	235.58	211.7-263.5	16.66	4.809	7.07	12
Carpometacarpus	117.21	105.5-131.4	8.65	2.234	7.38	15
Femur	162.82	140.3-175.8	10.91	2.728	6.70	16
Tibiotarsus	235.68	213.1-255.1	13.23	3.819	5.61	12
Tarsometatarsus	148.56	131.5-164.9	8.70	1.898	5.86	21

Table 3. Measurements (mm) and descriptive statistics for lengths (width for furculum) of the major axial and appendicular bones of *Harpia harpyja*.

Element	Mean	Range	SD	SE_x	CV	*n*
Non-paired elements						
Cranium + premaxilla	118.5	109.3-127.2	8.96	4.482	7.57	4
Mandible	85.6	79.5-92.8	6.31	3.156	7.37	4
Furculum	70.5	59.6-80.5	9.87	4.936	14.00	4
Sternum	128.7	117.3-135.4	9.45	4.727	7.35	4
Pelvis	133.3	119.7-147.4	13.00	6.502	9.76	4
Paired elements						
Scapula	102.6	94.4-111.7	7.85	3.927	7.66	4
Coracoid	75.7	69.3-82.9	6.16	3.079	8.14	4
Humerus	183.1	164.0-204.7	18.07	9.034	9.87	4
Ulna	215.3	187.5-229.0	25.84	12.920	12.00	4
Carpometacarpus	96.2	87.4-106.8	8.90	4.452	9.26	4
Femur	120.5	112.1-129.7	7.20	3.602	5.98	4
Tibiotarsus	173.6	155.5-192.3	17.08	8.542	9.84	4
Tarsometatarsus	109.3	101.3-117.8	7.53	3.763	6.88	4

Although the sample sizes were small, a trend towards bimodality was discernible in some of the distributions (Fig. 1A, B, C, D, L, M). The distributions for two indicators of body size, total head length (Fig. 1A) and femur length (Fig. 1L), were divided at subjectively assessed cut-points (groups indicated by horizontal lines in Fig. 1), and these a posteriori groups differed significantly (Student's t, unequal variances: head length, $t=10.907$, $P<0.001$); femur length, $t=6.799$, $P<0.001$). The observed trend and these differences suggested that the parent population contained two size classes which, judging from the continuity of most size distributions, overlapped. This suggested that the parent population was sexually dimorphic in size. Which was the larger sex could not be determined from the data presented here; it is usual in most members of the Accipitridae for the female to be larger, but in the Old World vultures, the male is larger (Brown & Amadon 1968).

The geographical distribution of the two nominal species as listed by Oliver (1955), the last worker to recognise both taxa, is summarised in Table 4. The type specimens for both

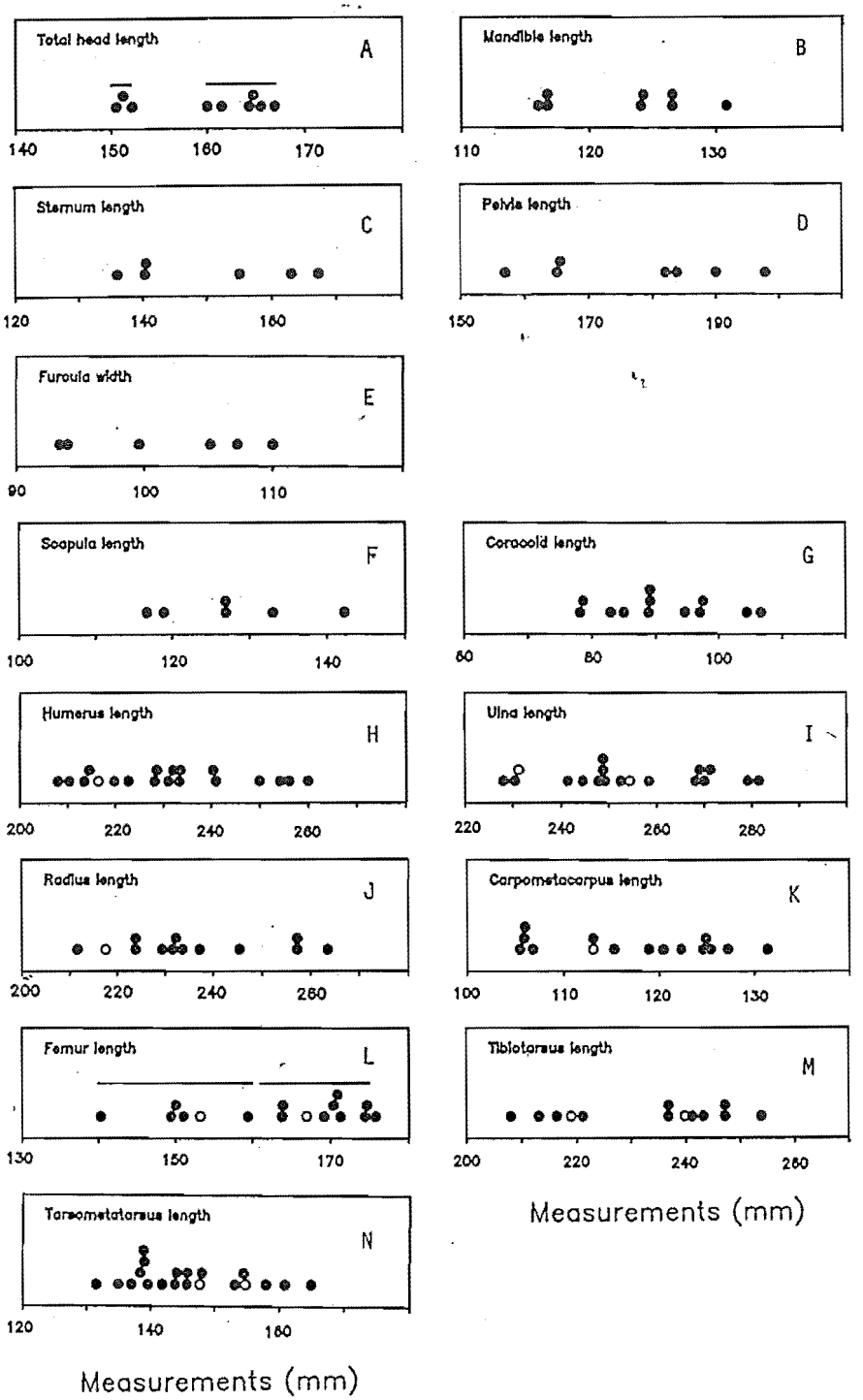

Figure 1. Dot distribution diagrams of lengths or width (mm) of major axial and appendicular bones referred to *Harpagornis moorei* and *H. assimilis*. Lengths are total lengths, taken over maximum extremities. Note different scales. Horizontal lines denote a priori groups used in statistical tests (see text). Open circles denote values for type material for the two nominal species.

Table 4. Localities from which bones attributed to *Harpagornis moorei* and *Harpagornis assimilis* have been recovered, as listed in Oliver (1955), the last publication to discriminate the distributions. Note that this is not (and is not intended to be) a complete list of localities for *Harpagornis moorei*: not only have several new localities been discovered since Oliver's work, material had been collected from other sites before then but was either unrecognised in collections, or Oliver did not locate the specimens. * = sites from which only a single bone has been recovered.

Site	*H. moorei*	*H. assimilis*
North Island		
Te Aute	x	
Waingongoro[1]		*
South Island		
Wairau Bar	x	
Lake Grassmere	x	x
Pyramid Valley	x	x
Banks Peninsula	*	
Glenmark	x	x
Motunau		*
Enfield	x	
Kapua		*
Dunstan	*	
Hamilton Swamp	x	x
Warrington		*
Castle Rocks	x	x

[1] The Waingongoro record (Mantell; Lydekker 1891) is doubtful; there is evidence that Mantell mixed the collections from Waingongoro with those he obtained from Waikouaiti, north of Dunedin (T. Worthy, pers. comm.). The Waikouaiti site is similar to several others in the South Island which have produced eagle remains recently, whereas there are no other records from the extensive midden, and associated dune, deposits in the North Island. The distribution of *Harpagornis moorei* will be discussed elsewhere.

taxa came from the same horizon in a stream-side swamp at Glenmark, North Canterbury (Haast 1872, 1874); they were only a few hundred metres apart (Haast 1874, 1879). Specimens referred to both taxa were recovered from five of the 14 sites listed by Oliver (1955). The taxa were represented equally (i.e., one of each) at four of the five sites where they occurred together. The genus was represented at five of the remaining nine sites by single bones. Therefore, sympatry was demonstrated, or could not be ruled out, at 10 of the 14 sites. Of the remainder, the record from Waingongoro has been questioned, the Wairau Bar material consisted only of claws, and artefacts made from bone fragments, and that from Enfield was removed to England and never described, or even listed, in the literature available to Oliver. If two species of large eagle were present in New Zealand, the evidence available to workers who recognised them, indicated that they were not only broadly sympatric geographically, but they also occurred in roughly even numbers in several areas.

At Honeycomb Hill caves, about 10 individuals have been identified, and these would probably, on Haast's or Oliver's criteria, have been assigned evenly to the nominal taxa (author's unpublished data). Two of the 6 individuals represented by femora at the Honeycomb Hill caves would have been within the range accepted by earlier workers for H. assimilis and 4 within that for H. moorei. Oliver (1955) gave the humerus length for *H. moorei* as 210 mm, as against 218 mm for *H. assimilis* which indicates some inconsistency in the referral of specimens to the nominal taxa even by those who accepted the distinction.

DISCUSSION

Not unexpectedly, the data presented here supported Haast's (1874) suggestion that *Harpagornis assimilis* cannot be separated taxonomically from *Harpagornis moorei* Haast, 1872. The pooled samples showed variation consistent with their being derived from one taxon. The variability in the length measurements was less than that expected if more than one species were represented in the samples and this has been used as a criterion for lumping nominal species taxa in subfossil birds by, for example, Cracraft (1976).

The two nominal taxa would also have enjoyed largely sympatric distributions. No other species-pair of very large eagles is known to be site sympatric over most of their ranges (Brown & Amadon 1968), or to co-exist in equal numbers at the same sites.

The degree of bimodality in the data was consistent with the suggestion that the population was sexually size dimorphic, as in most other

large eagles. In eagles, the female is the larger bird (Brown & Amadon 1968); Haast's guess that the smaller bird he named *H. assimilis* was a male of the species he had previously described was almost certainly correct.

The analysis showed that there was insufficient variability within the mensural data for the pooled samples to support distinguishing two taxa based on size, which was the sole character used by Haast (1874). Therefore, *Harpagornis assimilis* Haast, 1874 must be reduced to subjective synonymy with *Harpagornis moorei* Haast, 1872. Morphology was not included in the original diagnosis (Haast 1874), and comparison of the femur from the type series of *H. moorei* with that from the type series of H. assimilis revealed, as indicated by Haast (1874), that they did not exhibit more than individual variation (author's unpublished data).

The data presented here provide a formal basis for the present taxonomic situation (e.g., Kinsky 1970). The taxonomic conclusions and a classification of *Harpagornis moorei*, with a synonymy and designation of lectotypes, are given below.

SYSTEMATIC PALAEONTOLOGY

Order Ciconiiformes (*sensu* Sibley *et al.* 1988)
Family Accipitridae
Genus *Harpagornis* Haast, 1872

Type species, by monotypy, *Harpagornis moorei* Haast, 1872

Harpagornis moorei Haast, 1872

Harpagornis moorei Haast, 1872: 193; pl. X, fig. 1, 4, 5; pl. XI, fig. 1, 1a, 2, 5. -Haast, 1874: 62; pl. VII, fig. 1-6; pl. IX, fig. 1-3. -Owen, 1879: 141; pl. CV, fig. 1-3; pl. CVI, fig. 3-6; pl. CVII, fig. 1-7. -Haast, 1881: 234. -Lydekker, 1891: 25. -Hamilton, 1893: 92, pl. VII C, D. -Hamilton, 1894: 227; pl. XXIII, fig. 4. -Rothschild, 1907: 85. -Oliver, 1930: 392. -Lambrecht, 1933: 411, 707. -Oliver, 1945: 137. -Oliver, 1955: 604, (not illustration). - Brodkorb, 1964:272. -Kinsky, 1970: 78 (in list).

Harpagornis assimilis Haast, 1874: 64; pl. VIII, fig. 1-7. -Owen, 1879: 143 (as *H. moorei*); pl. CVI, fig. 1, 2, 4. -Haast, 1881: 232; pl. IX, fig. 1-4. -Lydekker, 1891: 25 (as ?synonym). -Hamilton, 1893: 92. -Hamilton, 1894: 227; pl. XXIII, fig. 1-3. -Oliver, 1930: 394, unnumbered figure (mislabelled *H. moorei*). -Lambrecht, 1933: 411 (as synonym). -Oliver, 1955: 605, unnumbered figure p. 604 (mislabelled *H. moorei*). -Brodkorb, 1964: 273 (as synonym) -Kinsky, 1970: 78 (as synonym, in list).

Harpagornis haasti Oliver, 1945: fig. 46 (lapsus).

TYPE DATA

Harpagornis moorei CMNZ AV 5104 (pt), left femur, 2 pedal ungual phalanges, 1 rib (missing), F. Fuller, Mar 1871, Glenmark. *Harpagornis assimilis* CMNZ, AV 5102, pelvis, right and left tarsometatarsus, right and left tibiotarsus, right and left femur, right humerus, right and left ulna, left carpometacarpus, left scapula, one rib, four phalanges, one ungual phalanx, Canterbury Museum party, Aug 1873, Glenmark.

DESIGNATION OF LECTOTYPES

To facilitate comparisons between the two nominal taxa, and association of other elements with the recognised taxon, it is desirable that the name be based on the element in the type series with the greatest number of potentially useful morphological features. For *Harpagornis moorei*, I designate as **lectotype** the left femur labelled TYPE catalogued as part of AV 5104 in the type collection of the Canterbury Museum. It is in perfect condition, with muscle scars clearly visible, and minimal abrasion. The 2 ungual phalanges marked TYPE, and rib (presently missing) become **paralectotypes**. The other material catalogued under AV 5104, and also labelled on the bones as TYPE in the same hand as the series above were not part of the original collection or included in the description and therefore have no taxonomic standing. The TYPE inscriptions on the bones are most likely post-description additions.

For the reasons outlined above, I also designate the left femur catalogued under AV 5102, in the Canterbury Museum, as **lectotype** of the name *Harpagornis assimilis* Haast, 1874. The other bones included under AV 5102, see above, all become **paralectotypes**.

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APPENDIX I

SPECIMENS OF *HARPAGORNIS MOOREI* AND *HARPIA HARPYJA* MEASURED FOR THIS STUDY, BY ELEMENT AND REPOSITORY

Harpagornis moorei

Cranium CMNZ, AV 5684, AV 5685; NMNZ, DM 2134, S 22473.1, S 23479, S 23611, S 27773, S 25580; OM, C 40.8. Mandible BMNH, unnumbered; CMNZ, AV 5323, AV 5685, AV 12355; NMNZ, DM 2134, S 23611, S 27773; OM, C 40.8. Furcula NMNZ, DM 2134, S 22472.1, S 23611, S 27773, S 23825; SM, unnumbered. Sternum CMNZ, AV 6177; NMNZ, DM 2134, S 22473.2, S 22473.3, S 27773; OM, C 40.8. Pelvis BMNH, 75.12.15.34; NMNZ, DM 2134, S 22473.4, S 22473.5, S 23030, S 27773; OM, C 40.8. Scapula BMNH, unnumbered; CMNZ, AV 5333; NMNZ, DM 2134, S 23051.2, S 27773; OM, C 40.8. Coracoid BMNH, 4; CMNZ, AV 13014; NMNZ, DM 2146, S 22472.2, S 22472.3, S 22653, S 23611, S 22653, S 23453, S 27773; OM, C 40.8. Humerus BMNH, 8, A423; CMNZ, AV 5102 (**paralectotype**, *Harpagornis assimilis*), AV 5333, AV 29361, AV 36396; NMNZ, DM 2143, DM 2145, DM 2146, S 22736, S 23030, S 23431, S 23432, S23433, S 23825 (3), S 27773; OM, C 40.8. Ulna BMNH, 12, 13; CMNZ, AV 5102 (**paralectotype**, *H. assimilis*), AV 5104, AV 5324, AV 5329, AV 36405; NMNZ, DM2134, S 22472.6, S 23030, S 23434, S 23436, S23437, S 23438, S 23825, S 23611, S 27773; OM, C 40.8. Radius BMNH, 14, A 423; CMNZ, AV 5104, AV 5329, AV 5333; NMNZ, DM 2134, S 22472.4, S 23825, S 23073.2, S 23440, S 23441, S 27773; OM, C 40.8. Carpometacarpus BMNH, 35, 36; CMNZ, AV 5102 (**paralectotype**, *H. assimilis*), AV 6291, AV 11163; NMNZ, DM 2134, S 22472.7, S 22653, S 23456, S 23457, S 23611, S 23825, S 25582, S 27773; OM, C 40.8. Femur BMNH, 10; CMNZ, AV 5102 (**lectotype**, *Harpagornis assimilis*), AV 5104 (**lectotype**, *Harpagornis moorei*), AV 28366; NMNZ, DM 2138, DM 2143, DM 2145, S 22472.9, S 23030, S 23462, S 23464, S 23611, S 23825 (2), S 27773; OM, C 40.8. Tibiotarsus BMNH, 16; CMNZ AV 5102 (**paralectotype**, *H. assimilis*), AV 5104, AV 5322, AV 5324, AV 5333; NMNZ, DM 2134, S 22472.11, S 22473.7, S 23467, S 23470, S 23611, S 27773; OM, C 40.8. Tarsometatarsus BMNH, 19, 93.1.30.21; CMNZ, AV 5102 (paralectotype, *H. assimilis*), AV 5104, AV 12263, AV 16221; NMNZ, DM 2134, DM 2137, DM 2139, DM 2143, S 22472.14, S 23073.1, S 23473, S 23474, S 23475, S 23825 (2), S 27773; OM, C 03.60, C 40.8.

Harpia harpyja

BMNH, 1872.10.25.1, 1862.3.19.14, 1862.3.14.19; NMNH, USNM 429223.

CHAPTER 3

8. CHAPTER 3

DISTRIBUTION AND HABITAT OF HAAST'S EAGLE *HARPAGORNIS MOOREI* HAAST, 1872

8.1 INTRODUCTION

The distribution and nature of fossil sites can provide information on the distribution, habitat, and habits of an extinct species. Among the many factors that must be considered are the distribution of suitable sites for fossilisation within and outside the species' potential distribution in life, the mode of deposition, disturbance and damage during decay and before material burial, the probability of discovering a site, the techniques of excavation, and objectives of any excavation of the site.

The reconstruction of the ecology of an extinct species, and of the life assemblage (biocoenosis) of which it was a part, necessarily stems from fossils of the animal and its associated death assemblage (thanatocoenosis), depends on at least three interdependent stages of inference that correspond to stages in the transition from a living community to a fossil sample (Clark & Kietzke 1967; Holtzman 1979). Information is lost at each stage, so working from the fossil sample towards the structure of the living community involves many assumptions, that may or may not hold under different conditions. The stages in palaeoecological analysis are: fossil assemblage analysis; taphonomic reconstruction; and palaeoecologic reconstruction (Holtzman 1979).

One way of subdividing the process is to separate the operations on the basis of level of representation. In the scheme outlined by Holtzman (1979), fossil assemblage analysis uses the fossil sample collected from a site to predict the composition of the whole fossil deposit at that site. Taphonomic reconstruction involves the reconstruction of the thanatocoenosis of which the fossil deposit is itself a sample. And palaeoecologic analysis is the reconstruction of the biocoenosis from which the thanatocoenosis was drawn (Fig. 8.1).

For a single species, the questions involved at each stage of the process were slightly different (Fig. 8.1, boxed points). The fossil assemblage analysis, which is aimed at community analysis, then becomes a fossil sample analysis in

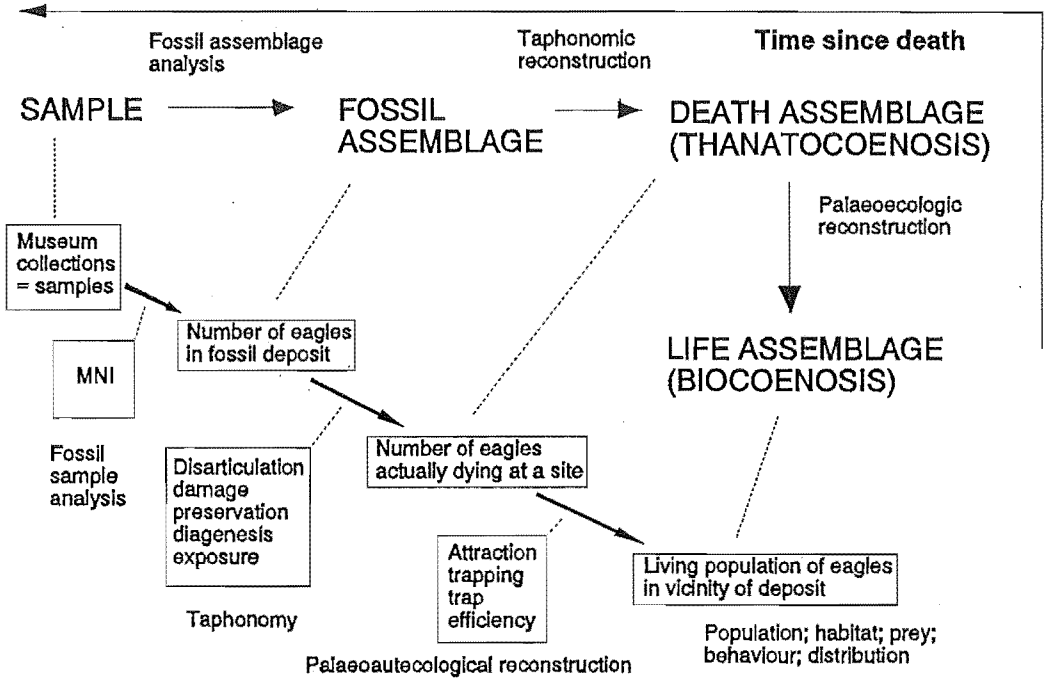

Fig. 8.1 Schematic diagram of stages in the reconstruction of the ecology of an extinct species, by analysis of fossil samples.

which the principal question is how many individuals of that species of what size range, are represented in the whole site. The taphonomic analysis of the processes of disarticulation, burial, preservation and exposure, can then be used to work out the number that actually died there. Finally, the palaeoautecologic analysis attempts to elucidate the factors in the living animal's habits and habitat that resulted in the sample of living individuals represented in the death assemblage.

Only recently have excavations of Quaternary fossil vertebrate faunas in New Zealand, other than those associated with archaeological projects, been accompanied by extensive faunal analysis. Leach (1979), on a Palliser Bay site, and Horn (1983), on Poukawa in Hawke's Bay, are examples of archaeologically based faunal studies. Purely palaeontological studies include those of Millener & Templer (1981) on a cave in the Waikato, and Millener (1984), Worthy (1987), and Worthy & Mildenhall (1989) on the Oparara caves. Most natural sites have been found by accident and visited only once. Several, including Holyoake Stream and Marfells Beach, were not excavated; bones were picked up from the ground surface. The ability of the collector to notice bones has played a disproportionately large part in the accumulation of available fossil samples, especially from dunes.

In the analysis of Quaternary vertebrate samples, the usual approach in New Zealand has been to estimate the minimum number of individuals (MNI) represented in a deposit. MNI was then used as an index of relative abundance of taxa in the palaeofauna (e.g., Holdaway 1990; Horn 1983; Leach 1979; Millener 1981; Millener & Templer 1981; Worthy 1984, 1987, 1990), a method developed by Sloan (1929) and Howard (1930).

The broad habitat requirements of living species represented in the fossil fauna, and any information on the vegetation present at the site during deposition, have then been used as bases for palaeoecologic interpretation, especially of the probable habitats of extinct taxa (Anderson 1983; Burrows 1989; Burrows *et al.* 1981; Holdaway 1989; Worthy 1990; Worthy & Mildenhall 1989). This approach has been successful insofar as a consensus is developing concerning the broader aspects of New Zealand palaeoecology, such as whether

grassland, scrubland, shrubland, or forest birds were more abundant, which species of the larger birds were more abundant in different areas, and whether faunal distributions and abundances changed substantially over time (Anderson 1990; Flux 1989; Holdaway 1990; Worthy 1990).

Other significant results have been the demonstration of intraspecific variation in size with time, and the presence or absence of sexual size dimorphism in moas (Worthy 1987). These findings have had important ramifications for systematic and palaeoecological studies (Worthy 1988, 1989, 1990).

Palaeoecological inferences also depend on the functional morphology of the animal. The functional morphology of *Harpagornis moorei* is discussed briefly in Chapter 5.

The present Chapter deals first with the geological, geographic, and temporal context in which fossils of Haast's Eagle have occurred. After summarising information available about each site, I describe aspects of the distribution of the sites with respect to the physical environment and vegetation patterns, and the absolute and relative dating of sites and levels within sites.

Then, the fossil sample is analysed to establish the representation of elements and the minimum number of individuals (MNI) at each site. These data are used to assess the modes of deposition at each site. Using the distribution of sites and their limiting dates and the number of birds, I then speculate on the rates of entrapment at different kinds of site. In the Discussion, I assess the distribution of Haast's Eagle in terms of the physical environment and vegetation patterns in New Zealand during the late Pleistocene and Holocene.

8.1.1 Definitions

Terminology and criteria for inclusion I use the term fossil for all bones found in Quaternary sites of any age. The distinction between subfossil (unmineralised bones) and fossils (mineralised bones) is blurred over the time range and nature of the New Zealand Quaternary deposits, and so is of little practical value.

Only identifiable fossils have been included; that is, those that can be assigned on morphological grounds (with further information from associated

material) to the taxon of interest. I have followed Holtzman (1979) in distinguishing between elements and specimens. An element is the smallest part of an organism that can be identified reliably in isolation. In studies of mammals, or where large faunas contain several similar taxa, many bones cannot be identified in isolation. The situation is simpler in New Zealand, where there is a comparatively small fauna. Once the problem of the second nominal species, *Harpagornis assimilis*, had been resolved (see Chapter 2A), most parts of the skeleton could be identified confidently, and previous errors corrected.

The suite of remains that can be attributed to one living individual constitutes a specimen. Holtzman's (1979) criterion is that the remains must include at least one identifiable element for them to be considered a specimen. In this study, the process could be reversed, i.e. previously unknown elements of the skeleton were identified by association with other material from a site. In many instances, a small residue of bones such as ribs, could be referred with confidence to a specimen, most of whose elements were instantly recognisable, even though there was evidence of transport within the site.

A few instances of misidentification of material by earlier workers were noted (see material lists).

Site versus locality A site is defined as a specific place and horizon within a deposit. In contrast, a locality is taken to be the geographic location of a site or group of sites. For example, the different fossil sources in the Honeycomb Hill Cave system are sites, but the cave system as a whole is considered a locality. Within the locality Glenmark, there are at least four distinct sites. These are separated by up to several hundred metres in space. Regardless of whether they are contemporary or up to several tens of thousands of years different in age, they constitute a single locality for analysis of geographical distribution.

8.2 SITE DESCRIPTIONS

8.2.1 General

Little information was available about most sites where eagle remains have been found. Haast (1872, 1874, 1879, 1881), Booth (1875), and Hamilton (1889, 1893, 1894, 1904) described some early sites in varying degrees of detail. Many of these sites were destroyed during early, unskilled excavations; others have been destroyed since or can no longer be located. Some sites, such as Hunterville (Drew 1896), were mentioned only in relation to other material, and some went unrecorded except as cryptic labels on bones (Waipapa Point). The lack of information, and often of the site itself, has also meant that it is difficult arrive at even an approximate date for some sites.

Material from some potentially important sites, such as Golden Point in Otago, where a nearly complete skeleton was recovered, has been lost. For others, such as Te Aute in Hawke's Bay, one of only four confirmed North Island occurrences of the eagle, the number of elements known in collections falls far short of the number reported from the excavation. Enfield, another important site, was so poorly documented (see e.g., Forbes 1892), and the material moved to Britain under such circumstances (Hamilton and Hutton, in letters to *Lyttelton Times*, 31 May 1892, p. 125), that the precise provenance of many bones now in the British Museum (Natural History) [now the Natural History Museum] will always be in doubt.

Although Hamilton (1893) provided a useful list, with dimensions, of material from all the sites of which he was aware, many of the earlier published records have vague references to "several" or "many" bones. Even where bones were described with some care, doubt remains as to how many, and which, bones were actually found (e.g., Haast 1881; Hamilton 1893, 1894, 1904).

The following section summarises available information about the sites.

8.2.2 Site descriptions by locality

Bones referable to *Harpagornis moorei* Haast, 1872 have been recovered from at least 41 separate sites in caves, swamps, estuarine deposits, river gravels, dunes, and Polynesian occupation areas, at 29 localities in the South Island and southern North Island of New Zealand. As noted above, material from some sites cannot be traced, for others the original description of the site or labels associated with the material do not allow an exact location to be ascertained.

A residue of material that cannot be ascribed to a particular site also exists. It is likely that most of this came from one or other of the known sites, and in a few instances other evidence has enabled a particular element to be attributed to a particular site. However, much can only be listed as 'no locality'.

All dates are based on the Old (Libby) T½ (5568 years) unless noted otherwise. In lists of materials, "pt" indicates one of a series of bones catalogued under the same number.

Descriptions of identified sites follow, in alphabetical order, by locality.

8.2.2.1 Albury Park (Fig. 8.2)

NZMS260 J38/330662 41°11′30″S 170°47′50″E.

McCulloch & Trotter (1979) described this site as a "spring-hole swamp with bones of moas, eagle, etc., mostly in a peat matrix." The site is in a valley cut in limestone. There is a line of sinkholes on the ridge above, to the north. The site was probably Holocene, based on a ^{14}C date (NZ1726) of 7 390±160 years BP.

Material Tip of premaxilla, CM, no number, collected B McCulloch, 1971; humerus, L, same data; tibiotarsus, R, same data.

8.2.2.2 Cannibal Bay (Fig. 8.3 A-C)

NZMS260 L27/421092 41°07′25″S 172°11′30″E.

This is a surface collection, from an archaeological site (NZ Arch Assn S184/4), on dunes behind the beach. There is no record, apart from the Archaeological Association site record number in the Canterbury Museum register to confirm human association. The dunes were backed by forest until clearance for European farms, and isolated forest trees are still present. Other, similar, beach

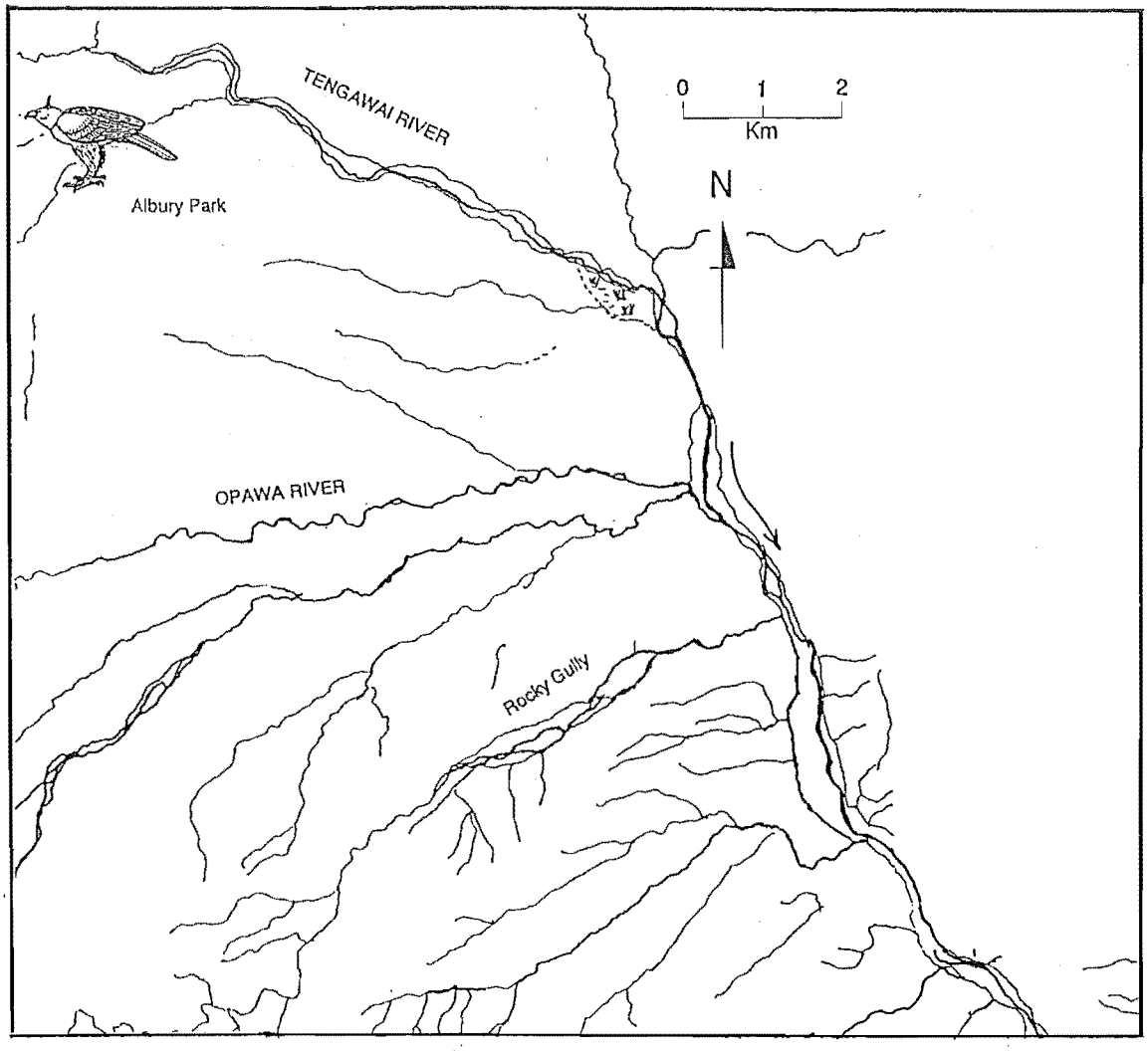

Fig. 8.2 Albury Park site, showing topography and drainage pattern in immediate area.

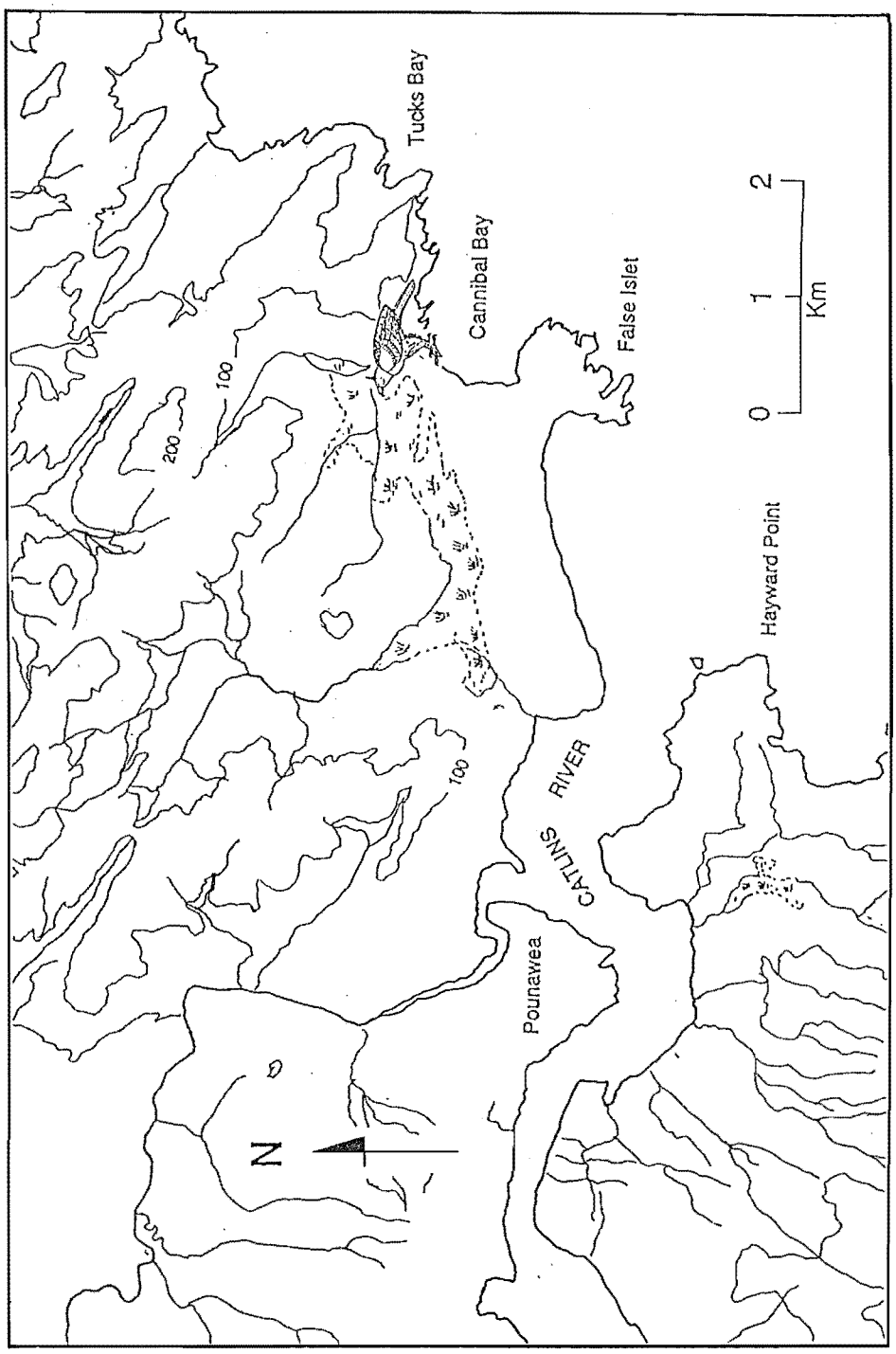

Fig. 8.3A Cannibal Bay site, Catlins District, eastern Southland, showing topography and drainage pattern in immediate area.

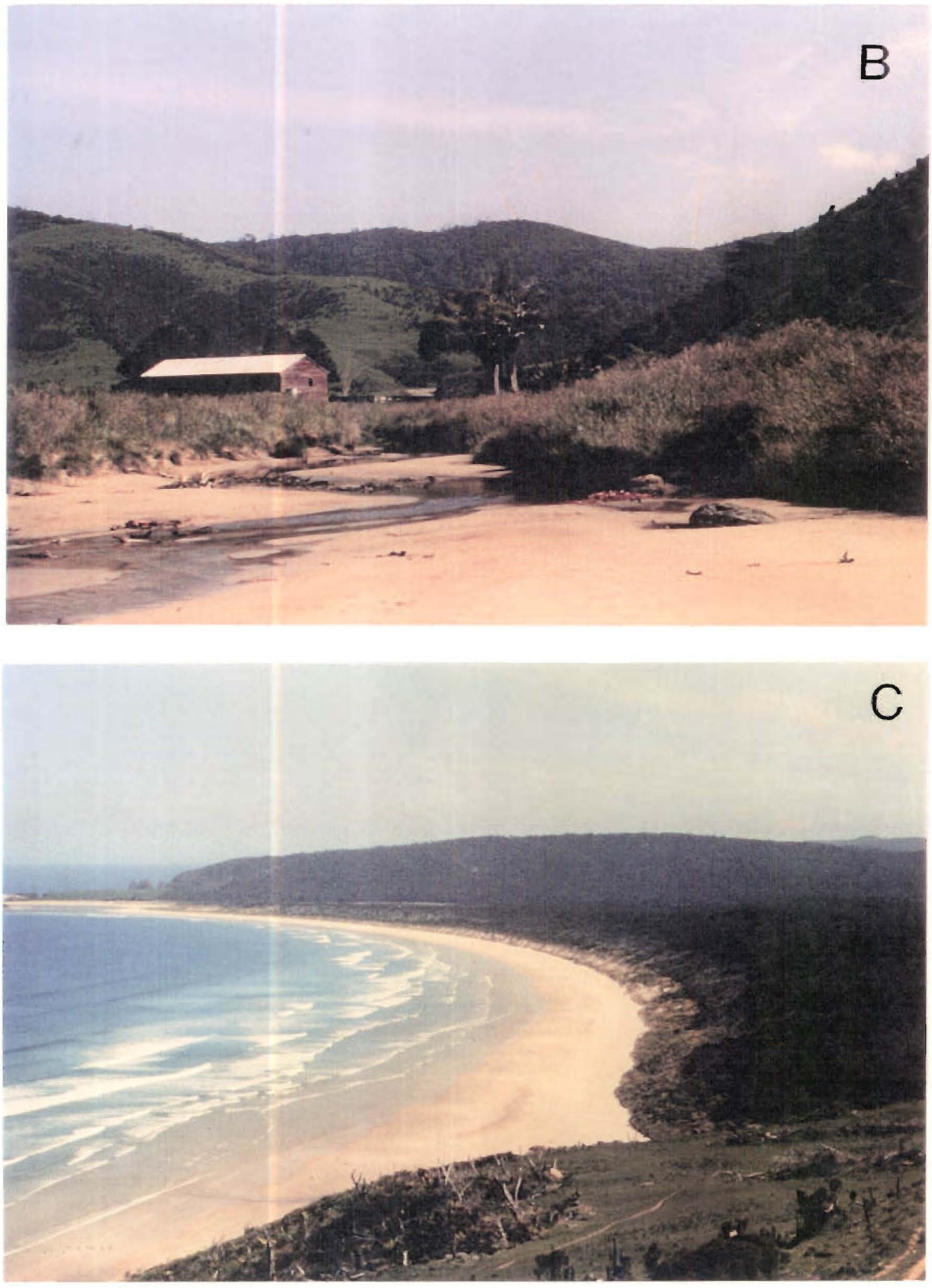

Fig. 8.3 (B, C) **B**, view to northwest of dunes and stream mouth at eastern end of bay, and forest remnants on surrounding hills (December 1988); **C**, view south along coast at Tautuku Bay, 25 km southwest of Cannibal Bay (December 1988), showing intact beach-forest ecotone typical of southern coastline in the area before Polynesian and European deforestation.

sites occur along the Catlins coast. The dunes are probably ≤ 6 000 years old (see above). A ^{14}C date from a cultural horizon was 390±39 years BP; it is not known what, if any, association the eagle bone had with any cultural remains.

Material S184/4, cranium, CM, AV 34466.

8.2.2.3 Castle Rocks (Fig. 8.4 A-D)

NZMS260 H46/606108 46°28′00″S 169°45′20″E.

Hamilton (1893, 1894) described intensive excavations in this fissure amongst pillars and fallen boulders in an outcrop of limestone, west of the Oreti River, and just east of an extensive swamp. The deposit was discovered by a Mr Mitchell in the late 1880s. It was excavated by Messrs Mitchell, Barnhill (the owner of Castle Rock Station), and Augustus Hamilton in 1892 and 1893 (Hamilton 1893, 1894). The main fissure (Fig. 8.4D) was a pitfall trap for flightless birds. It was wide enough to allow eagles entry, but narrow and deep enough to prevent their escape (i.e. a no-return trap). The bones were found in firm calcareous silt that afforded good preservation. This, and the unusual care taken with the excavation (Hamilton 1893) resulted in many small bones, including vertebrae and quadrates being recovered. The material is now in OMNZ and NMNZ. No ^{14}C date is available for Castle Rocks material, but Worthy (1988) suggested an age of 2 000-3 000 years from its location.

Material Carpometacarpus, L, R, NMNZ, DM 2134pt; coracoid, R, NMNZ, DM 2134pt; cranium, NMNZ, DM 2134pt; furcula, R, NMNZ, DM 2134pt; mandible, NMNZ, DM 2134pt; manus 1st phalanx, ?, NMNZ, DM 2134pt; pelvis, NMNZ, DM 2134pt; quadrate, R, NMNZ, DM 2134pt; radiale, ?, NMNZ, DM 2134pt; pygostyle, OMNZ, C 40.8pt; radius, R, NMNZ, DM 2134pt; ribs (parts of 19), NMNZ, DM 2134pt; scapula, L, R, NMNZ, DM 2134pt; sternum, NMNZ, DM 2134pt; tarsometatarsus, L, NMNZ, DM 2134pt; tibiotarsus, R, NMNZ, DM 2134pt; ulna, L, ulna, R, NMNZ, DM 2134pt; ? humerus, L, NMNZ, DM 2145pt; carpometacarpus, L, R, OMNZ, C 40.8pt; coracoid, L, R, OMNZ, C 40.8; cranium, OMNZ, C 40.8; femur, L, R, OMNZ, C 40.8pt; fibula, R, OMNZ, C 40.8; furcula, OMNZ, C 40.8; humerus, L, R, OMNZ, C 40.8; mandible, OMNZ, C 40.8; manus II/1, R, OMNZ, C 40.8pt; metatarsal 1, R, OMNZ, C 40.8pt; pedal phalanx I/1L, I/1R, I/2L, I/2R, II/1?, II/2L, II/2R, III/1?, III/2?, III/3a?, III/3b?, III/3c?, III/4?, IV/4?, IV/5a?, IV/5b?, pelvis, OMNZ, C 40.8; prefrontal, R, OMNZ, C 40.8pt; radius, L, R, OMNZ, C 40.8; rib - sternal bL, sternal cL, sternal dL, vertebral fR, vertebral gL, vertebral unc aL, vertebral unc aR, vertebral unc bL, vertebral unc bR, vertebral unc cL, vertebral unc cR, vertebral unc dL, vertebral unc dR, vertebral unc eL, vertebral unc eR, vertebral unc fL, sternal aL, OMNZ, C 40.8pt; scapula, L, R, OMNZ, C 40.8pt; sternum, OMNZ, C 40.8pt; tarsometatarsus, L, R, OMNZ, C 40.8pt; tibiotarsus, L, R, OMNZ, C 40.8pt; ulna, L, R, OMNZ, C 40.8; vertebra - caudal a, b, c, d, e, cervical a, b, c, d, e, f, g, h, i, j, dorsal a, b, c, d, e, f, g, OMNZ, C 40.8pt.

8.2.2.4 Dunstan Range (Fig. 8.5)

NZMS260 G39/40 44°35′00″S 169°45′00″E.

The only information about this site is the comment by Hamilton (1893) that he had "a specimen from the Dunstan Range". This is taken here to be the northern spur of the St Bathans Range, east of the Lindis Pass, as on NZMS series maps, and not to the Dunstan Mountains between the Clutha and Manuherikia Rivers. The most likely type of site in this area is a rock overhang. The specimen has not been dated.

Material Tarsometatarsus, R, NMNZ, DM 2136.

8.2.2.5 Enfield (Fig. 8.6)

NZMS260 J41/429723 45°02′01″S 170°52′20″E.

This was a spring-hole swamp, filled with peat. The deposition regime was similar to that at Makirikiri (Worthy 1990), but the area is now drained and dry (McCulloch & Trotter 1979). The site is in a broad downland valley inland from Oamaru; the map reference given above and in Table 8.1 is from McCulloch & Trotter (1979). Forbes (1892) and Hutton (1896) briefly described the site. In 1891, the bone deposit was discovered in a small swampy gully leading into a tributary of Waiareka Creek. The landowner, W Meek, discovered moa bones when first ploughing the valley in August 1891, and the site was excavated by H O Forbes in the same year. Forbes (1892) published a brief description of the site and listed some species of bird from it, but he took most of the collection to England shortly afterwards and published nothing more about it. Hutton (1896) presented measurements of moa bones from the deposit. All bones from this deposit have a characteristic dark brown to black stain.

Excavation 1: about 0.9 x 0.9 m x 1-1.3 m deep; entirely in peat. "*Cnemiornis* and *Harpagornis* bones ... in abundance", and "several hundreds of moas of all ages" (Forbes 1892: 417).

Excavation 2: 6-7.5 m further up the gully; about 2.1 x 2.1 m x 1-1.2 m deep, in peat, with bottom in bluish clay. Contained the "largest deposit of moa bones"; as well as "numerous bones of the giant buzzard and of the great extinct goose" (Forbes 1892: 417).

Excavation 3: About 27 m further up from excavation 2; "not so large as the other two" (Forbes 1892: 417) but also 1-1.2 m deep; in peat, with bottom in bluish clay. Contained moa.

Excavation 4: "A few feet" (Forbes 1892: 417) further up the gully from 3, same dimensions as 3; in peat, bottom in bluish clay, with a small amount of fine silt. This pit contained only moa.

Water was reached at about 1.2 m in all pits, and the bluish clay was "charged with water" (Forbes 1892: 417). No other deposits were found by extensive probing around the area in which the pits were dug. Moa crop contents and gizzard stones were found, and none of the bones was waterworn.

A ^{14}C date of 2 020±70 years BP was obtained from moa bone collagen from this site, which confirmed its late Holocene age.

Material Radius, R, CM, AV 5329pt; tarsometatarsus, R, CM, AV 5329pt; ulna, L, CM, AV 5329pt; Carpometacarpus, L, BMNH, none; carpometacarpus, R, BMNH, 36; coracoid, L, BMNH, 3; coracoid, R, BMNH, 4; cranium, BMNH, 93.1.30.1; femur, L, BMNH, 10; femur, R, BMNH, 11; fibula, L, BMNH, 17; fibula, R, BMNH, 18; furcula, BMNH, 4; humerus, L, BMNH, 8; humerus, R, BMNH, 9; mandible, BMNH; pedal phalanx, BMNH; pedal phalanx, BMNH; pedal phalanx, BMNH, A424; pedal ungual phalanx, L, BMNH, 20; radius, L, BMNH, 14; radius, R, BMNH; scapula, L, BMNH, 6; scapula, R, BMNH; sternum, BMNH; tarsometatarsus, L, BMNH, 19; tarsometatarsus, R, BMNH; tibiotarsus, L, BMNH, 16; tibiotarsus, R, BMNH, 15; ulna, L, BMNH, 12; ulna, R, BMNH, 13; carpometacarpus, BMNH, R 3184; humerus, L, BMNH, A 423; radius, L, BMNH, A 423pt; pelvis, BMNH, A 424; coracoid, R, CM, AV 5334, CAST; furcula, L, CM, AV 5335, CAST.

8.2.2.6 Glenmark Creek (Fig. 8.7 A-C)

NZMS260 N34 921992 (Type) 43°01′00″S 172°47′00″E (see also Table 8.1).

The complex of sites at Glenmark, in North Canterbury, is at once one of the most important of eagle localities, and one of the most difficult to interpret. It is important as the type locality for both nominal species, and because deposits of two widely differing ages have been reported (Haast 1872, 1879). It is difficult to interpret because Haast's various descriptions do not tally in all respects, and there no maps of the area were published at the time. In addition, the detailed description of the sites given by Haast (1879), is difficult to reconcile with the map reference provided by McCulloch & Trotter (1979). Haast's description is made more confusing by its apparent reversal of chronological order, to suit the order in which the geography is described.

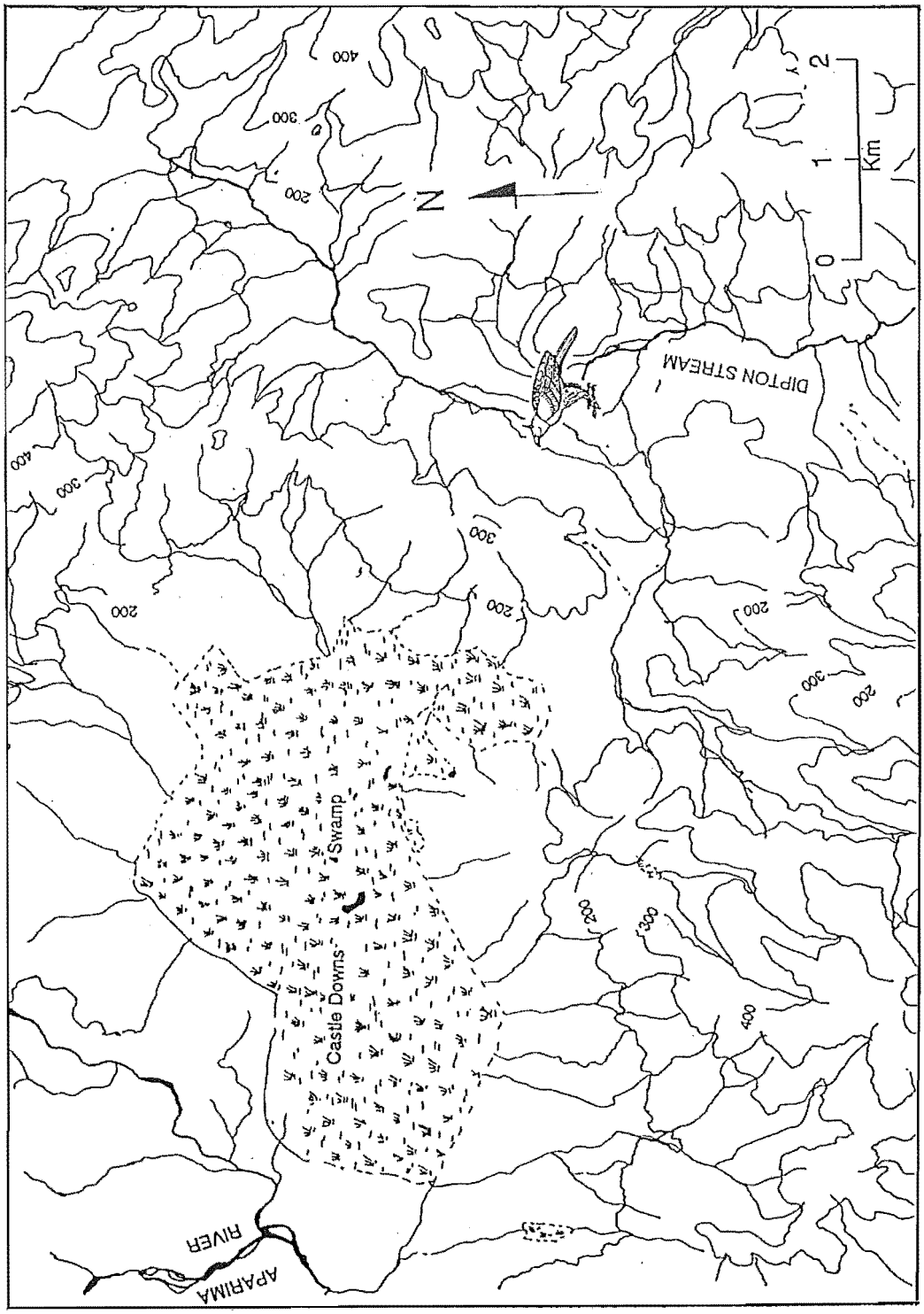

Fig. 8.4A Castle Rocks site, western Southland, showing topography and drainage pattern; note subdued relief and proximity to extensive swamplands.

Fig. 8.4 (B, C) **B**, General view of Castle Rocks outcrop from the northwest; **C**, detail of gaps and fissures described by Hamilton (1893). Photographs December 1988.

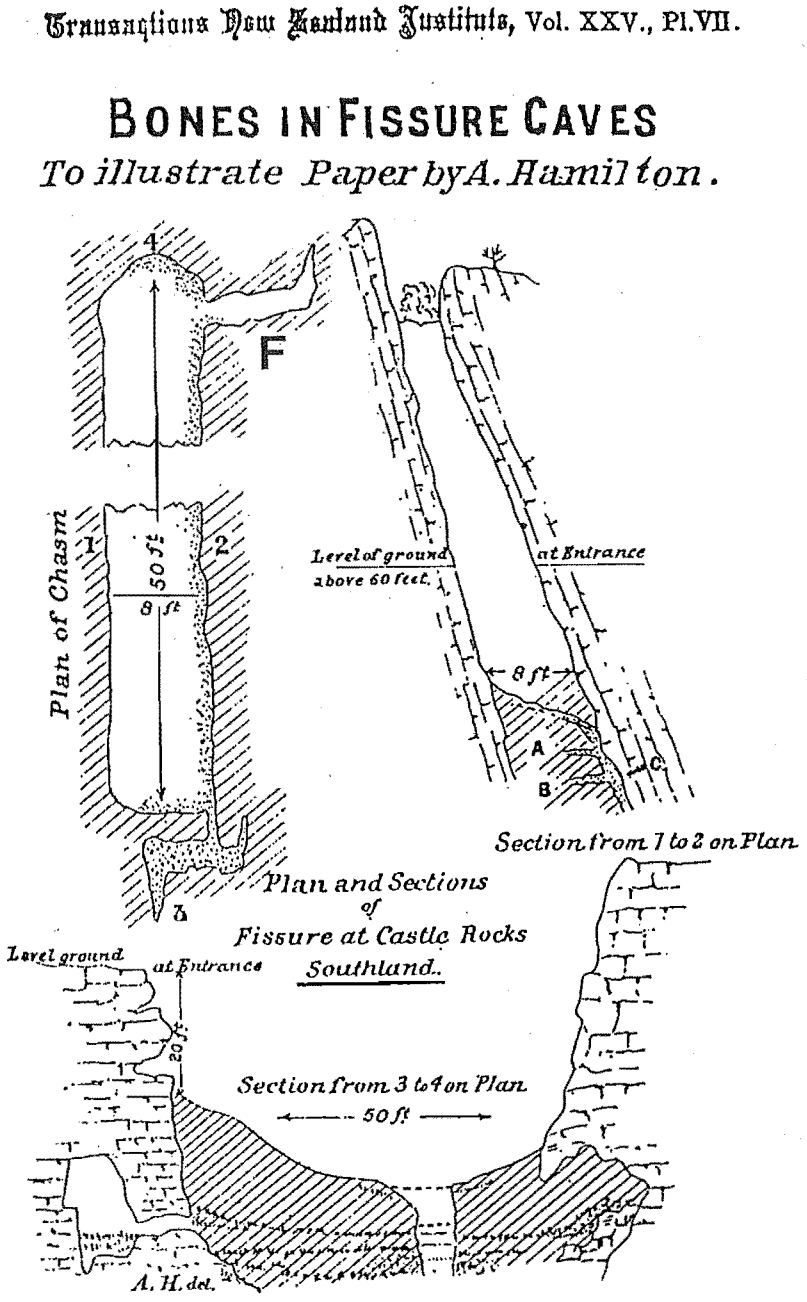

Fig. 8.4D, Plan of fissure excavated by Hamilton and others in 1891 and 1892 (Hamilton 1893: pl. VII).

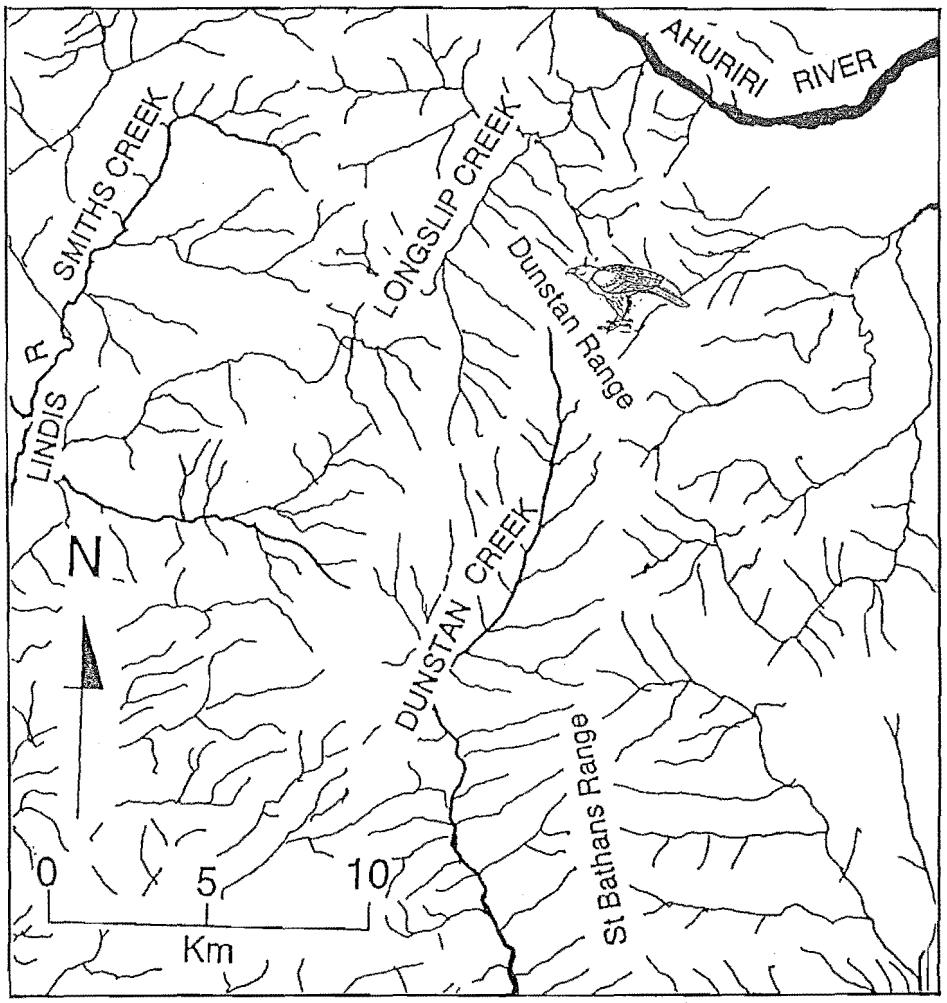

Fig. 8.5 General area of Dunstan Range site, central Otago, showing topography and drainage pattern.

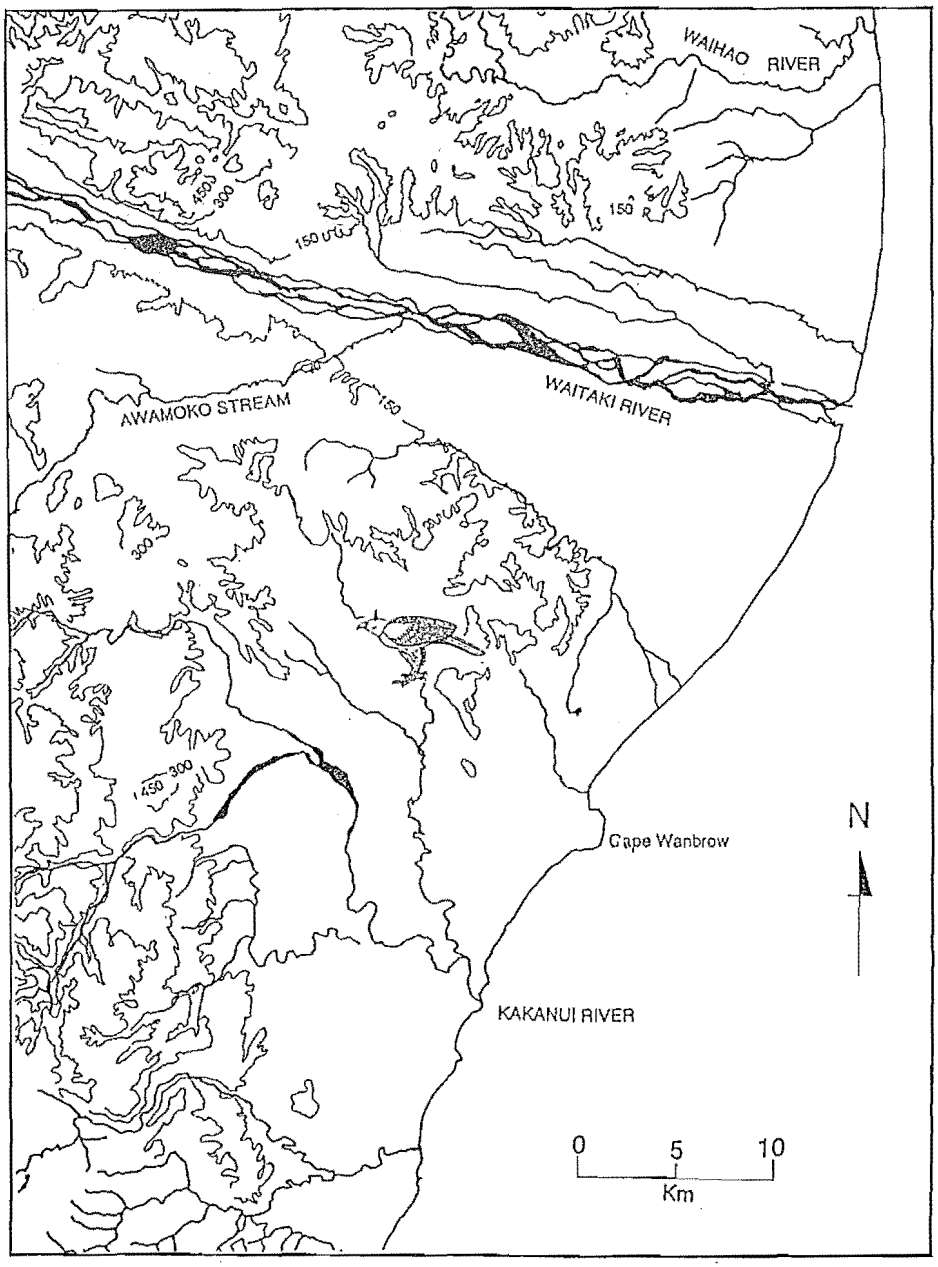

Fig. 8.6 Enfield site, showing topography and drainage pattern in immediate area.

Haast gave three separate descriptions of the Glenmark deposits. The first (Haast 1872) is very brief, and refers to the excavations of March 1871, in an area about 9 m square, and dug to a depth of 1.5-1.8 m. This excavation, whose exact location is not given, is the type locality of *Harpagornis moorei* Haast, 1872. In the same paper, Haast referred to a "fragment of a right humerus ... found together with a considerable quantity of moa bones in a small watercourse about two miles [3.2 km] from Glenmark". This is probably CM AV 9556 "Glenmark Creek 1873". Later (Haast 1874), he stated the latter site was a gravel section about 1.6 km above Glenmark Station. In the same paper, Haast mentioned the "lower portion of a metatarsus" of an eagle from "a similar older post-pliocene bed [to that where the humerus was found] situated close to Glenmark, and he described the results of excavations done between March 1871 and June 1873, at and near the site of the first discovery. More eagle bones were found further down the swampy stream bed from the original site; Haast (1874) ascribed these to the same individual represented by the first bones. They were found 1.8-2.1 m below the surface, at the base of the lacustrine deposits, among "remains of decaying swampy vegetation". There was also "drift timber" and many moa bones.

The material on which Haast (1874) named *Harpagornis assimilis* was found "Some time after" the second series from which the first specimen was excavated. The new site, the type locality of *H. assimilis*, was "on the left [eastern] bank of the Glenmark Creek, and opposite the spot previously alluded to" [i.e. the type locality of *H. moorei*]. This appears to mean that the type locality of *H. moorei* was on the right [western] bank of Glenmark Creek. The bones from the west bank were found near each other, above a layer of clay near the bottom of the lacustrine deposit, 2.1-2.4 m below the surface (Haast 1874). They were associated with "a considerable quantity" of moa bones. The second series of excavations probably took place in July 1872 (Haast 1879: 155).

The most complete description of the whole area is that of Haast (1874), pages 442 et seq. Haast first described the valley of Glenmark Creek, then described and discussed the various deposits in an upstream-downstream, or north to south, sequence. The northernmost site was about 1.6 km upstream of the homestead where the valley is narrower and the stream "flows in a narrow

channel either cut in limestone rocks or in post-pliocene alluvium" up to 21 m thick. At this point, several deposits of moa bones were found, along with material of *Aptornis*, and "a fragmentary humerus of *Harpagornis*". These bones were "covered at least with 60 ft [18 m] of subangular river shingle" (Haast 1879) and were "very heavy and impregnated with carbonate of lime".

About 400 m further downstream, towards but still north of the homestead, was another section exposed "in a nearly vertical cliff, on the left [eastern] bank". This section was described as follows [metric units converted from Haast's Imperial]:

[4.88 m] sands, often ferruginous, repeatedly alternating with layers of mostly small river shingle

[0.61 m] sandy peat, much compressed; with moa skeleton

[0.91 m] ferruginous sands, sometimes argillaceous

[1.07 m] river shingle, with a ferruginous matrix

[1.37 m] argillaceous sands

[1.22 m] rather coarse river shingle, on bluish micaceous sands.

Further downstream again, and near the deposits from which most of the moa bones were obtained, Haast described the creek as making "a sharp bend, flowing at nearly right angles to the direction of the valley, from the eastern to the western side". In doing so, it exposed a section, as follows:

[2.43 m] loess

[1.22 m] small river shingle (sandstone and limestone pebbles)

[0.30 m] sandy silt

[1.83 m] small river shingle, well stratified

[0.45 m] peat; with many moa bones

[3.05 m] river shingle cemented by a ferruginous matrix, plus an unknown depth obscured by recent sediments and talus.

The layers dip about 7 degrees towards the centre of the valley, where they appear horizontal."

The next passage is somewhat obscure as to where exactly it refers: "There is however a small inclination down the valley. Nos 3, 4, and 5, are here of much broader dimensions, the peat bed being nearly three feet [0.91 m] thick. In the

last mentioned layer, we obtained not only nearly every species of Dinornithidae, but also a few remains of *Cnemiornis* and *Aptornis*, together with a broken femur of *Harpagornis*."

Whether this is the same bone referred to as a "metatarsus" by Haast (1874) is not known; it probably is, but neither a femur nor a tarsometatarsus which could be this bone has been identified in any collection. Haast (1879) noted that all the bones from this peat layer were "very heavy and fossilized from calcareous matter filling their pores"; he emphasised the differences between these bones and those found in the superficial deposits further down the valley.

Haast seemed to be describing a position downstream from the section about which he gives details, but how far is not clear and can only be surmised from the description of the next site. This is stated to be about one hundred yards [90 m] downstream from where the femur (or tarsometatarsus) had been found. Here, a small stream or "rill" flowing down from the eastern side of the valley "loses itself in the swampy ground at the top of the terrace ... Close to the bend of Glenmark Creek". This bend is apparently the sharp east to west bend mentioned earlier, as there are several other bends and none that could be uniquely described as 'the bend'.

This description places the site on the streamside terrace on the eastern side of Glenmark Creek. Haast's party excavated an area of about 500 x 200 feet [152 x 61 m] in which moa bones occurred "in patches". A considerable quantity of vegetation in the form of tree trunks occurred there, and where the small rill entered the swamp, there was "sometimes a quite a network of timber, often of very large size, lying on the bottom." The stratigraphy was described as follows:

[1.22-2.13] m black peat

[0.61-0.91] m impure black peat, on a clay base; peat with a reddish hue, particularly when associated with moa bone; containing also "flax leaves, seeds, and stems of raupo, and pieces of drift timber of various kinds". The floor was uneven, with the clay bottom near the surface of the ground in several places near the centre. It was at this site that "portions of a skeleton of *Harpagornis assimilis* were found. The type locality of that taxon is therefore on the true left (eastern) bank of Glenmark Creek, above the homestead.

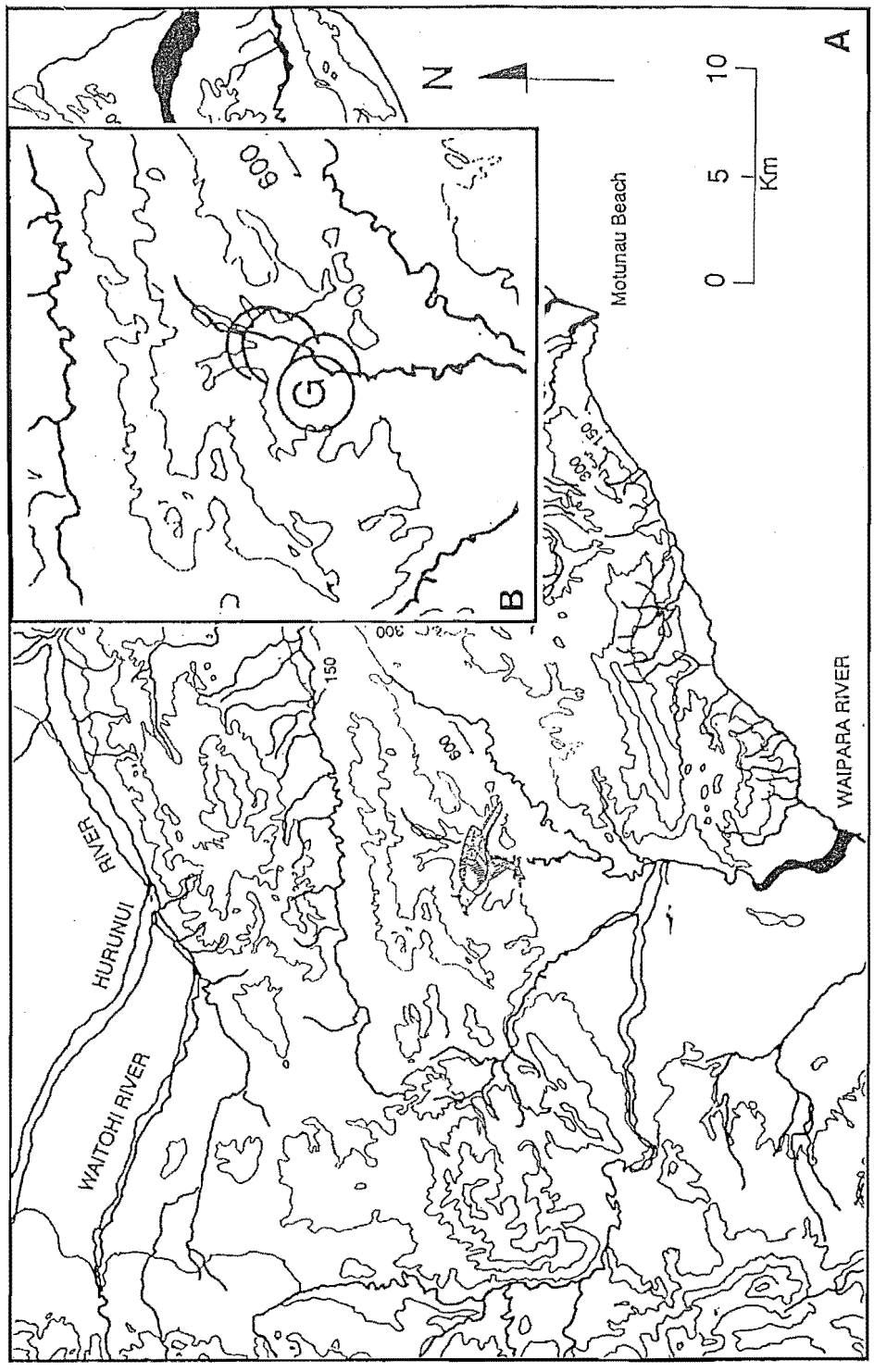

Fig. 8.7 (A-C) A, Glenmark area, showing topography and drainage pattern. B, Location of four sites in the Glenmark locality, as interpreted from Haast's (1872, 1874, 1879) descriptions.

Fig. 8.7C View towards southeast of largest remaining exposed section on east side of Glenmark Creek, probably the section described in Haast (1874, 1879). 'Peat' layer that produced moa and eagle bone near bottom of visible sequence, just above stream level. Type material for both nominal taxa was obtained from the valley fill sediments downstream from this section.

The final site described was "opposite to these [i.e. the extensive deposits where the type series of *H. assimilis* was found] on the right bank of Glenmark Creek [where] a small water-course joins the latter. Here the stream banks for about 90 m above the confluence averaged 15 m wide, and were composed of peat beds similar to those on the eastern side of the valley. The beds were 2.43-3.65 m deep, with drift logs near the base, and many moa bones. "However the most remarkable discovery made consisted of the bones of *Harpagornis Moorii* [sic]" (Haast 1879). This confirms that the type locality of *Harpagornis moorei* was a peat deposit on the right, or western, bank of the Glenmark Creek.

To summarise, eagle bones were found at four separate sites in the valley of Glenmark Creek. At two of these, single bones were found in peat layers or lenses under considerable thicknesses of gravels and clays; both sites were probably on the left, or eastern, bank of the creek. There is still a large exposure where the creek makes a sharp turn to the west, at map grid reference S68/144196. The humerus shaft is in the Canterbury Museum; the other bone, described variously as a tarsometatarsus or a femur, has not been located. The confusion about the identity of the bone suggests that it was misplaced sometime between 1873 and 1879.

The other two sites were more extensive, and on opposite banks of Glenmark Creek. An area matching the general description in Haast (1879) occurs a few hundred metres downstream from the large exposure mentioned above, at map grid reference N34/921992 [S68/141191]. Here, Waterfall Stream enters from the west and there is a small unnamed stream on the eastern side of the valley. The valley broadens, and old drains are still visible. The road has been cut into the streamside sediments, and may have obliterated the type locality of *Harpagornis moorei*.

This interpretation does not agree with the grid reference (NZMS 1 S68/147178) for the Glenmark site given by McCulloch & Trotter (1979). It places the site on the west bank of Glenmark Creek, at the base of the ridge opposite the present homestead. While there may have been some excavations in that area, it does not match the descriptions detailed above. If the reference is a lapsus for 147187, it would be in much better agreement with the type

locality of *Harpagornis assimilis*, being on the slope above the confluence of Waterfall and Glenmark Creeks. Neither combination of numbers places the site where it can be the type locality of *Harpagornis moorei* which was clearly on the right (western) bank of Glenmark Creek.

Two ^{14}C dates from Glenmark both indicate a Holocene age, so probably refer to the main lake swamp deposit. The dates - 7 110±109 (NZ4943) on moa bone, and 2 730±70 (NZ1729) years BP - also indicate that the site trapped moas over an unusually long time span for a swamp deposit. It was unlikely that the older date referred to either of the two Glenmark Creek sites, because the material from there was apparently in poor condition, was far more limited in number than that from the main sites, and should have been far older, based on the stratigraphy.

Material **Glenmark/East side** Carpometacarpus, L, CM, AV 5102pt; femur, L, R, CM, AV 5102pt; humerus, R, CM, AV 5102pt; pelvis, CM, AV 5102pt; scapula, L, none; tarsometatarsus, L, R, CM, AV 5102pt; tibiotarsus, L, R, CM, AV 5102pt; ulna, L, R, CM, AV 5102pt.
Glenmark/West side Femur, L, CM, AV 5104pt; fibula, L, CM, AV 5104pt; fibula, R, CM, AV 5104pt; pedal ungual phalanx, CM, AV 5104pt; radius, L, R, CM, AV 5104pt; scapula, L, R, CM, AV 5104pt; tarsometatarsus, L, R, CM, AV 5104pt; tibiotarsus, L, R, CM, AV 5104pt; ulna, L, R, CM, AV 5104pt; pedal ungual phalanx, CM, AV 5104pt; pedal ungual phalanx, CM, AV 5104pt.
Glenmark Creek Humerus, R, CM, AV 9556.
Glenmark Unknown site Pedal phalanx, R2/1, CM, AV 26534; vertebra, CM, AV 5327.

8.2.2.7 Golden Point Mine (Fig. 8.8 A-C)

NZMS260 I42/084365 45°21′05″S 175°25′40″E.

This site was in a stream fan swamp, in the deep valley of Deep Dell Creek, a tributary of the Shag River. Parker (1897) reported that a "nearly complete skeleton" of the eagle "had been sluiced out of Messrs N & G Donaldson's claim". Scars from sluicing are still visible on the southern side of the creek near the abandoned mine buildings; there is a small swampy area on the northern bank, slightly upstream, where rushes may hide other workings. This would put the site in the area photographed in December 1988 (Fig. 8.8C), but its exact location, and hence the stratigraphy, are unknown.

Sluicing was used at the site for only a short time, around 1896, after which the mine was worked from adits driven into the steep hillsides. The valley walls open out on to a rolling peneplain surface above. The eagle skeleton was apparently deposited in the Otago University Museum by T J Parker in

September 1896, but material from the site could not be found in the Otago Museum collections.

Moa bones were recovered along with the eagle skeleton. They were mentioned in a note read at the monthly meeting of the Otago Philosophical Society by Hamilton, but the note does not seem to have been published (Hamilton 1897).

Material None has been located.

8.2.2.8 Hamilton Swamp (Fig. 8.9 A-C)

NZMS260 H42/862468 45°15′10″S 170°09′30″E.

Booth (1875) described the site at Hamilton's Diggings in considerable detail, and included a plan and a section (Fig. 8.4C). He excavated it with Hutton in 1874, and the site was destroyed in subsequent mining operations. Originally, the site was on an area of flat ground, about 180 m square, and occupied a small area around a spring in a former pond that had been drained during mining operations nearby. The section was (direct metric equivalents):

[0.30-0.60 m] black peat, with blackish silt

[0.90-1.20 m] blackish silt, with bones

[0.30 m] fine whitish clay, very soft, somewhat elastic, with streaks and patches of "a red substance"

[0.60-2.43 m] bluish sandy micaceous clay

[3.00-9.00 m] water-worn quartz pebbles

The deepest part of the pond area was near the spring, and most of the bones were found there in a crescentic area about 12 m long by 5 m wide and from 0.60 to 1.2 m deep. Booth excavated a second site later (Booth 1877), but it did not contain eagle bones. Haast (1881) described several of the eagle bones found at this site, but again was vague as to exactly how many there were.

The stratigraphy suggests a late Holocene age for the main deposit. A second deposit nearby (Booth 1877) did not yield eagle bones and was nearly two metres beneath the clay basement of the first. This suggests that the second deposit was considerably older than the first, but no dates are available for either.

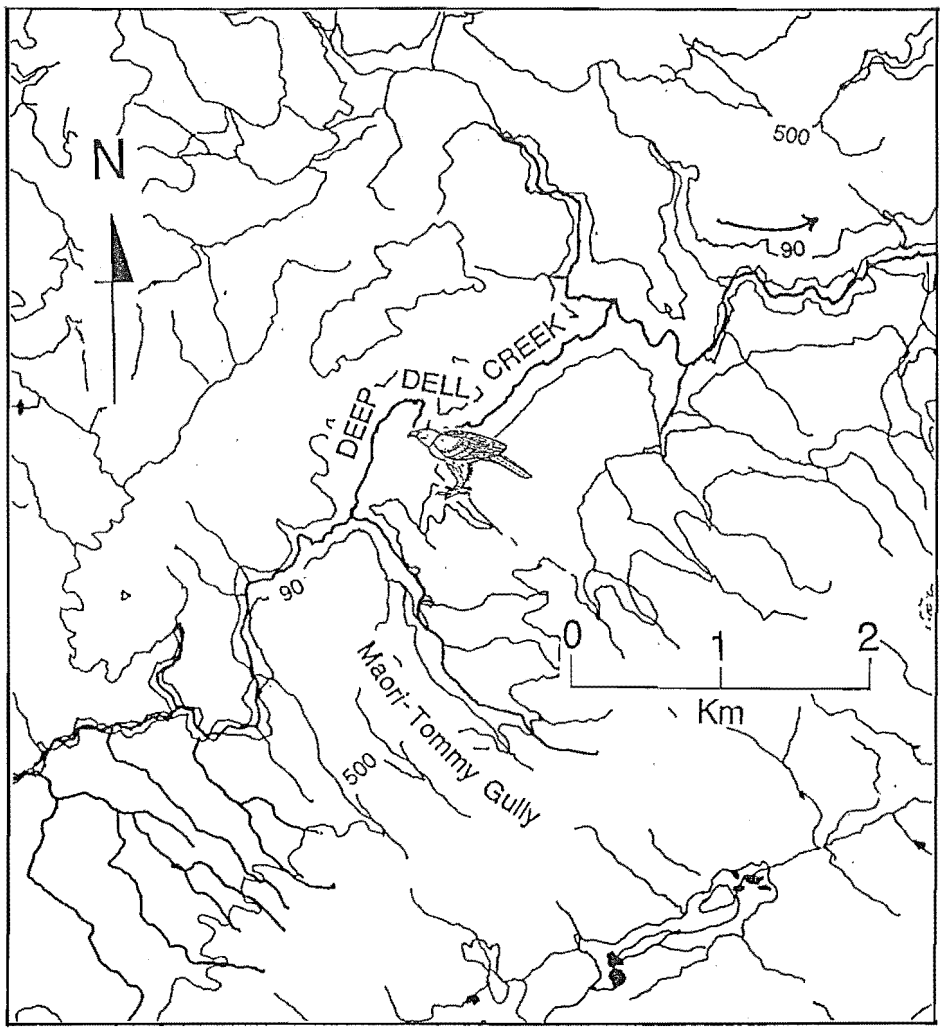

Fig. 8.8 (A-C) Golden Point Mine site, near McCrae's Flat, Otago: **A**, location, showing topography and drainage pattern.

Fig. 8.8 (B, C) View northwest over Deep Dell Creek, with preserved mine buildings middle distance at left, sluicing area behind and to left of large conifer near centre of view; note low relief of peneplain into which Deep Dell Creek has cut its valley; C, remains of sluice working face at Golden Point Mine, area cut out reaches back to behind camera position, abandoned drive into gravels to right of figure.

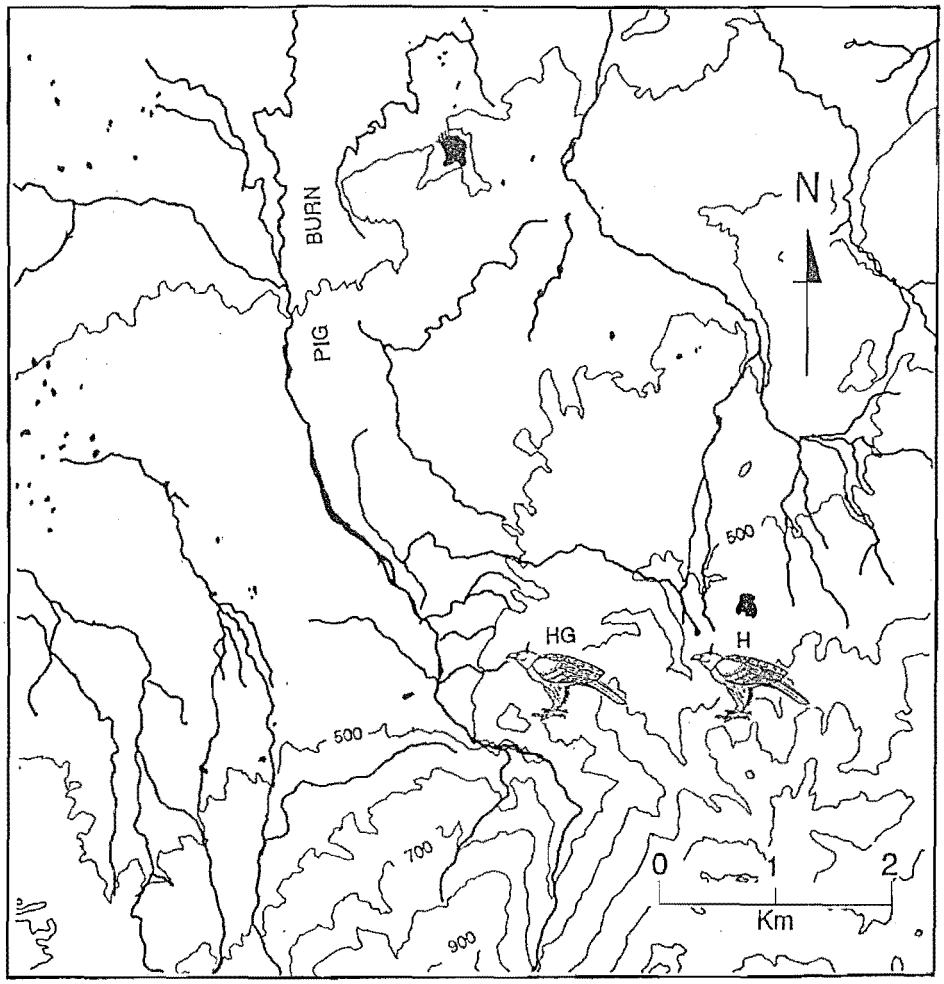

Fig. 8.9 (A-C) Hamilton Swamp and Hamilton Gully sites, on the northwestern margin of the Rock and Pillar Range, central Otago: A, location, showing topography and drainage pattern in immediate area.

Fig. 8.9B View northwest across flooded sluice workings which have obliterated eagle site. Range in background is typical of the area, and similar to the Rock and Pillar Range, on which Hamilton Swamp lies. Photograph, December 1988.

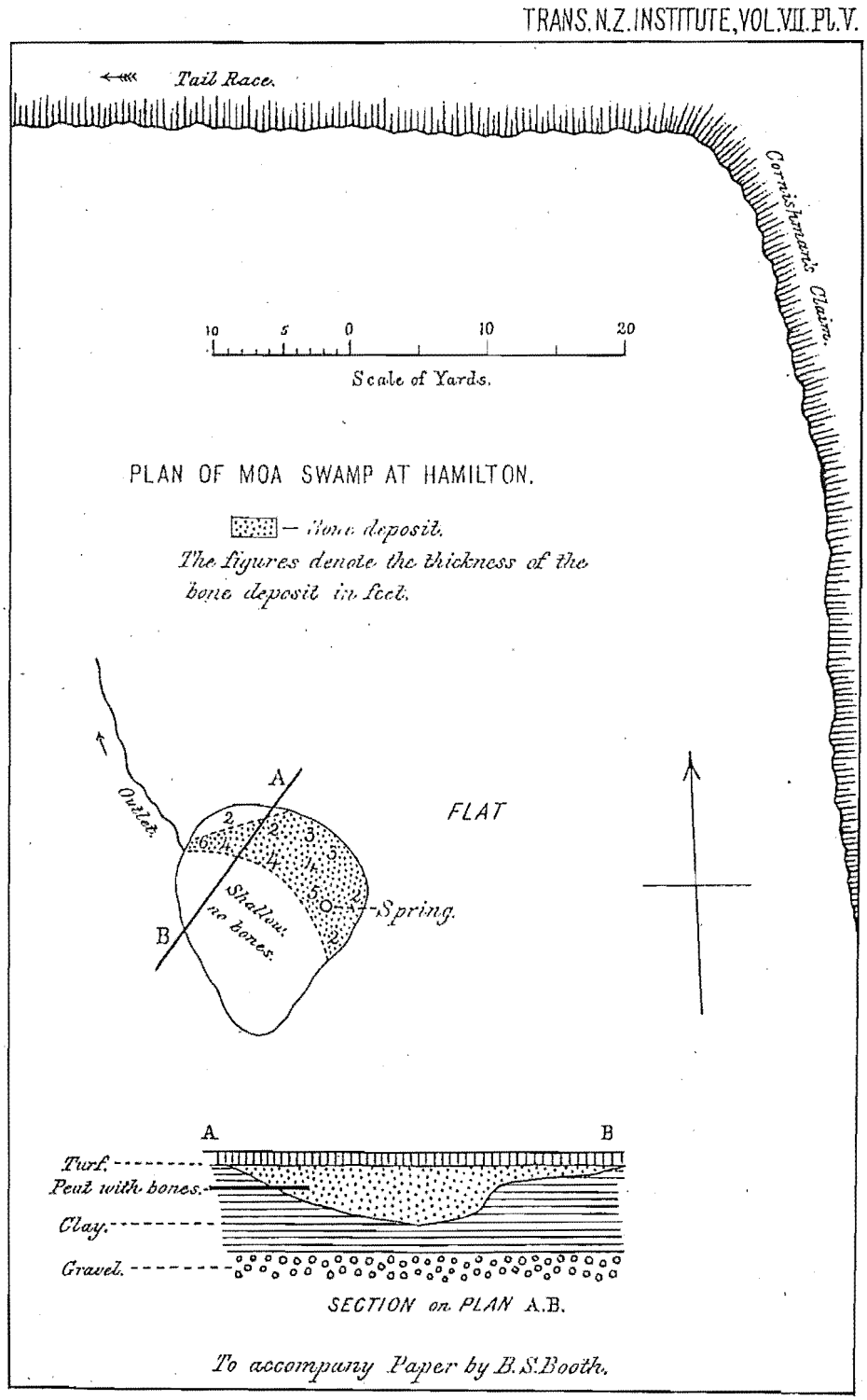

Fig. 8.9C Plan and section of first Hamilton site, from Booth (1875).

Material Carpometacarpus, AIM 574pt; pedal ungual phalanx, AIM 574pt; radius, AIM574pt; scapula, AIM 574pt; femur, L, OMNZ, unnumbered; pedal phalanx, I/2, OMNZ, unnumbered; pedal phalanx, IV/4 or III/3, OMNZ, unnumbered; carpometacarpus, L, CM, AV 6291; tarsometatarsus, R, CM, AV 5324pt; tibiotarsus, L, BMNH, A 2119; tibiotarsus, R, CM, AV 5324pt; ulna, L, OMNZ, unnumbered; ulna, R, CM, AV 5324pt; ulna, R, CM, AV 9555; mandible, CM, AV 5323; ? pedal ungual phalanx, AIM 574pt.

8.2.2.9 Hamilton Gully (Fig. 8.9A)

NZMS260 H42/845469 45°15′10″S 170°08′10″E.

Another site near the Hamilton Swamp is noted briefly by Haast (1881). This was "in a gully, about 1 mile [1.6 km] from Hamilton Swamp". The distal right femur "evidently extracted from a loess bed" is in AIM. Other material is catalogued under the same number (AIM 574; B J Gill, pers. comm.), and it is uncertain whether it too (see *Material* below), came from the gully site, or Hamilton Swamp itself.

About 1.5 km west of Hamilton Swamp is a valley with extensive gold workings dating from this period. It may be the area alluded to by Haast, and co-ordinates for it are included in Table 8.1.

As the site cannot be located on present evidence, no date can be assigned to it.

Material Femur, AIM 574pt.

8.2.2.10 Holyoake Stream (Hawkes Cave) (Fig. 8.10 A-C)

NZMS260 N26/017216 41°01′00″S 172°56′00″E.

Bones were collected from the surface layer of a fissure on the northern side of Holyoake Stream in January 1946. Bones were apparently visible from the ground surface outside the fissure (H Belton, pers. comm.), suggesting that it was either shallow, or the entrance was relatively open. I visited the area with T H Worthy in August 1990, but the most likely fissures in the area described had recently been filled in by heavy machinery. Several fissures were inspected, but no surface deposits were located. The site is likely to be late Holocene in age, because of its open nature, and because the material had survived surface exposure.

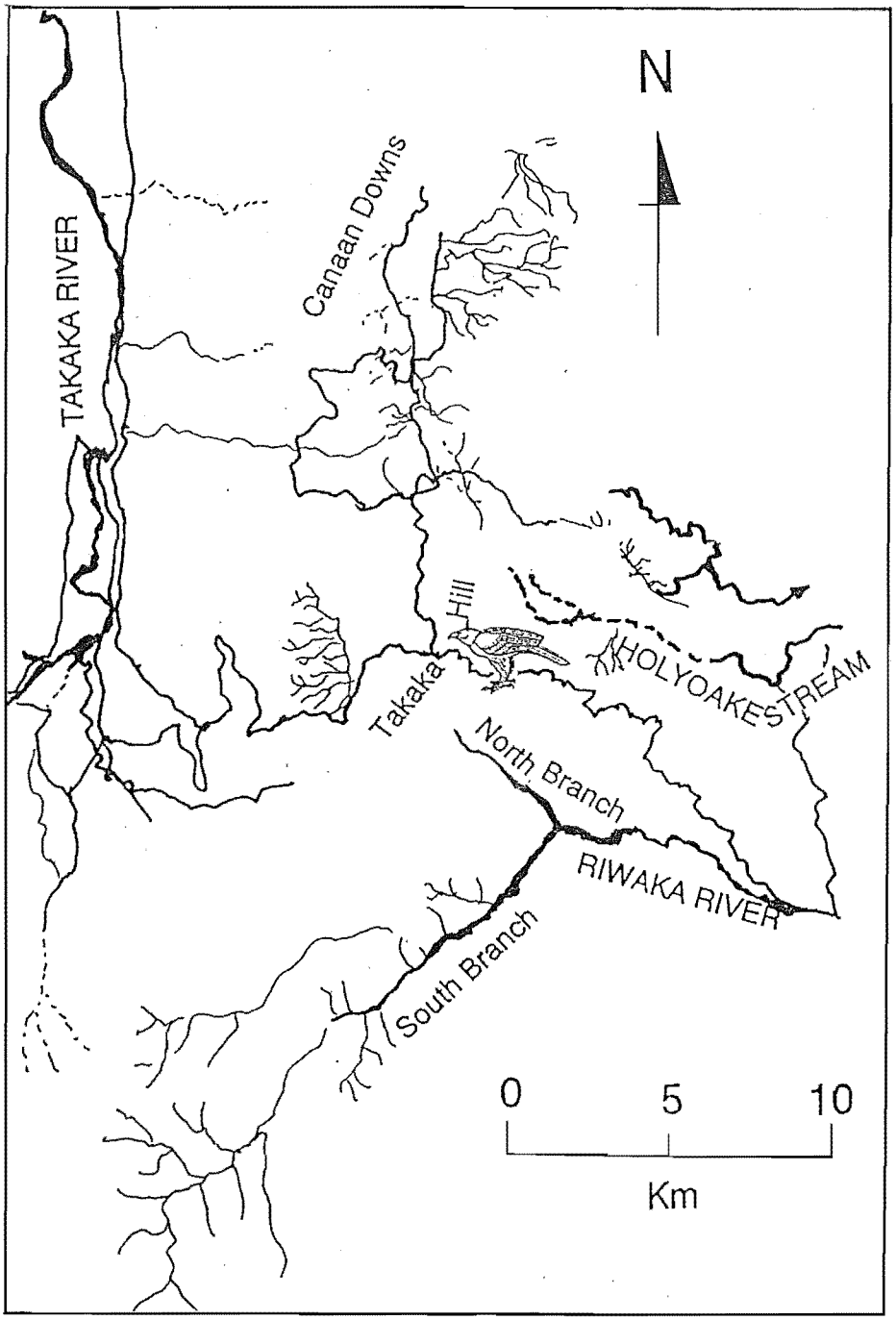

Fig. 8.10 (A-C) Holyoake Stream site, Takaka Hill, Nelson: **A**, location, showing topography and drainage pattern, with distribution of karst within the Holyoake Stream dry valley (from Williams, in Soons 1982: fig. 6.15). Most of the drainage in this catchment is subterranean.

Fig. 8.10B Entrance to Hawkes Cave: entrance is surrounded, and covered, by trees growing in doline. Ground surface in this area has eroded up to 1 m since removal of forest cover in early 1900s. View looking north. Photograph March 1991.

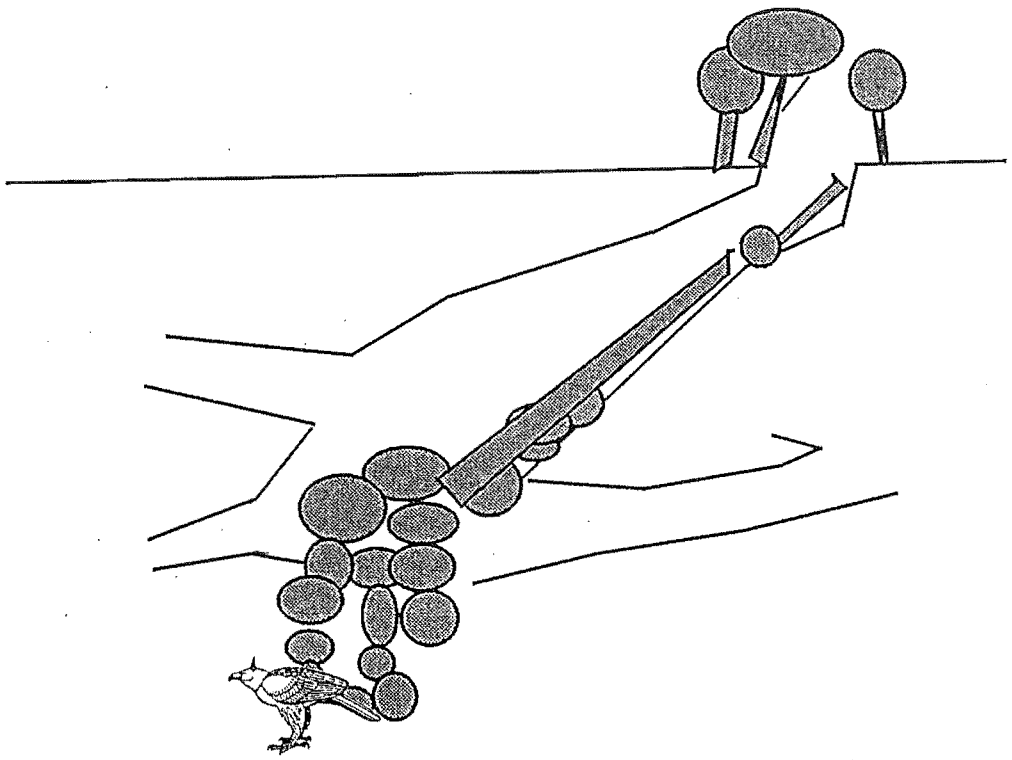

Fig. 8.10C Diagrammatic section of Hawkes Cave entrance area. Cave mouth is about 6m x 10 m, with a 3 m drop to the steep boulder slope. The eagle bones were found in a mud layer, in a small chamber at the bottom of the boulder pile; boulders 1-2 m in diameter.

Eagle bones were recovered from Hawkes Cave, near the head of Holyoake Stream, on 24 March 1991 by RNH and T H Worthy. Only smaller elements, such as pedal phalanges, carpometacarpi, and vertebrae, were recovered. The only remnants of large elements that may have been expected to survive at the site were the distal extremities of both tibiotarsi, which had been broken off as they were embedded in fine mud. The representation of elements suggests that the whole skeleton was present, and that most of it had been 'souvenired' at some time since the cave was first visited in the 1900s.

The physical nature of the site conforms in general with the memories of H Belton, but positive identification with that Holyoake Stream site is not now possible on that basis. However, the dimensions of the elements recovered in 1991 are exactly as expected for those elements based on the cranium size, and the cranium is from a very small individual. This suggests that Hawkes Cave, a well-known and easily accessible cave, is the Holyoake Creek site, and that the major elements, apart from the cranium are now either held privately, or have been discarded. The 1991 collection, comprising more than 50 elements, will be deposited in the NMNZ collection.

If the identification of the site with Hawkes Cave is correct, the date is probably early Holocene at the latest, based on faunal evidence, and the deposit structure (RNH, T H Worthy, unpublished data).

Material Cranium, CM, AV 9554; [other uncatalogued material, to NMNZ].

8.2.2.11 Honeycomb Hill (Fig. 8.11 A-E)

NZMS260 L27/421092 41°07′25″S 172°11′30″E.

This complex of rich sites includes AR144, E entrance, Eagle Roost, Graveyard, His Cave, and Hives Extension. Material previously identified as belonging to *Harpagornis moorei* from Unit Hole was reidentified as being from *Cnemiornis*. The large cave system was first explored in 1976 by P Wood of Westport and the Buller Caving Group; the first scientific visit was by a Canterbury Museum party in 1980 (Millener 1984). Excavations by National Museum parties, sponsored by the then New Zealand Forest Service and later the Department of Conservation, of many sites within the various caves that make up the system, have been

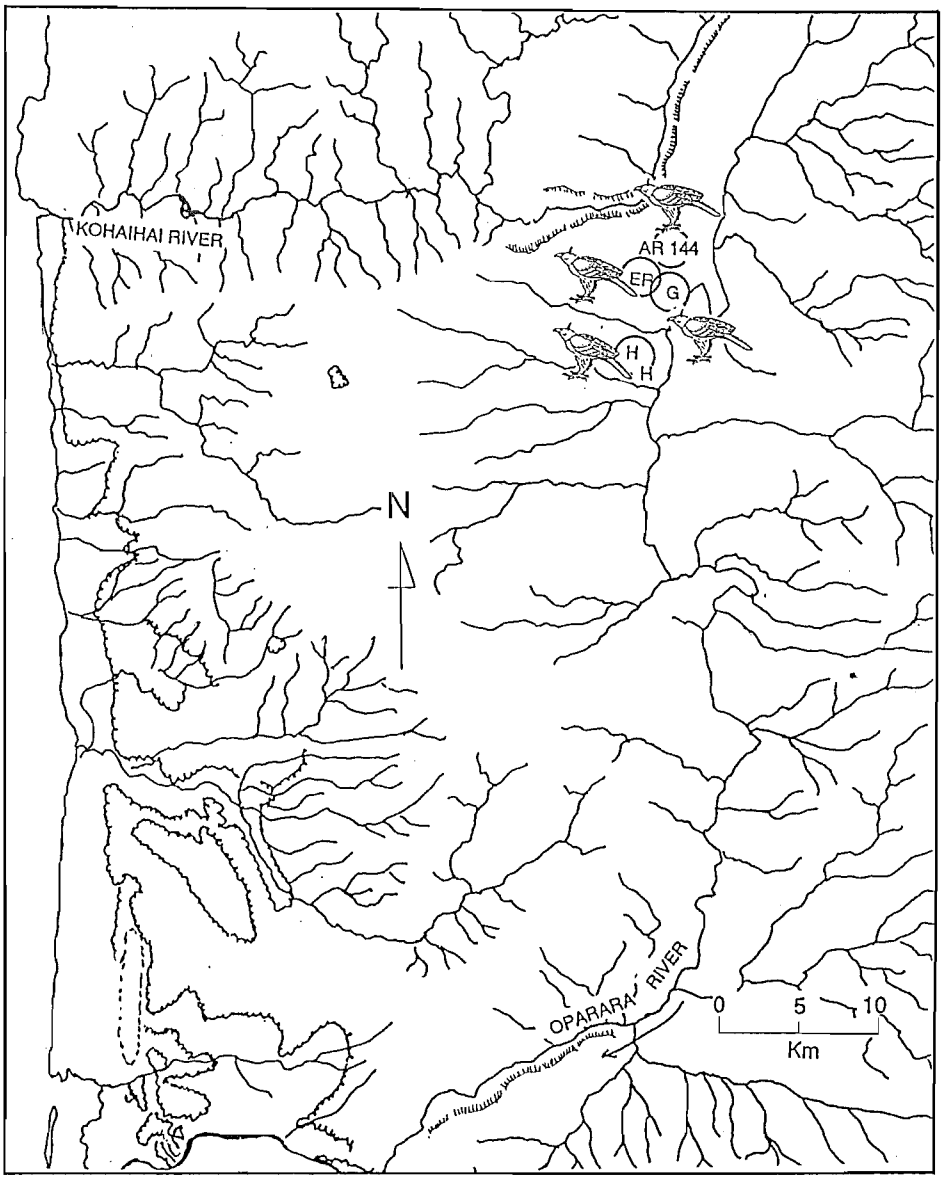

Fig. 8.11 (A-E) Honeycomb Hill, Oparara Valley, sites. **A**, Location, showing topography and drainage pattern. When the deposits containing eagle remains were forming, this valley was several km further from the sea, and 100-150 m higher above sea level. General map of cave system from Worthy (1991).

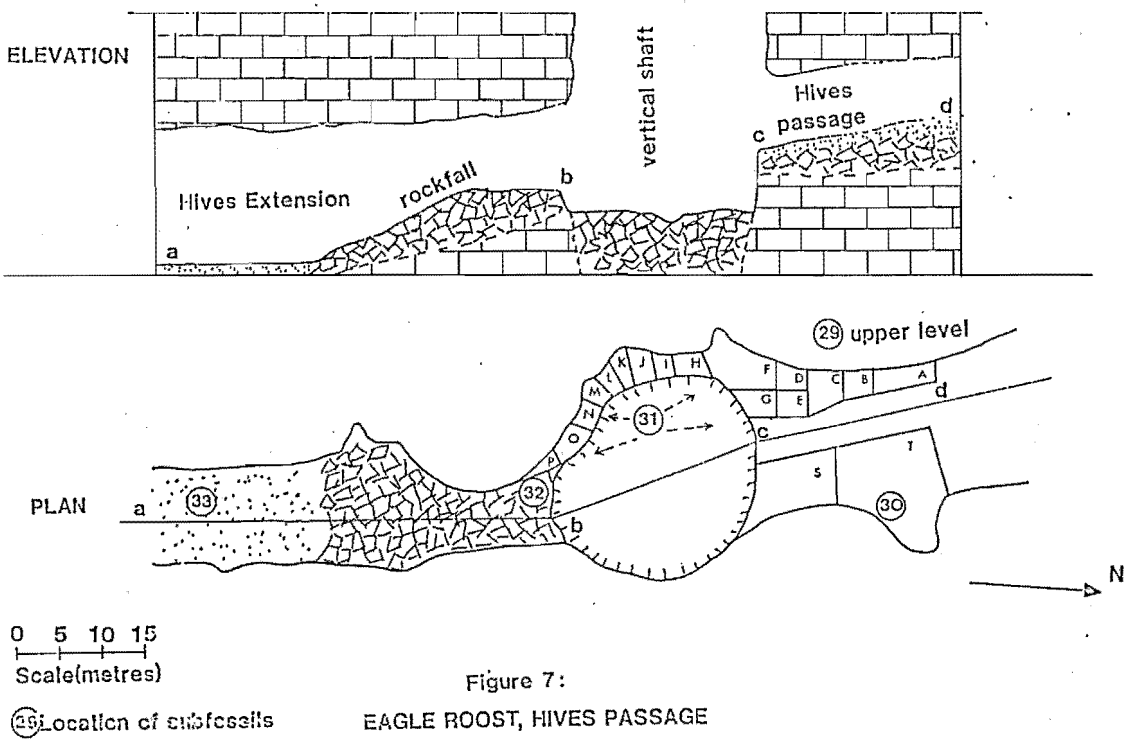

Figure 7:
EAGLE ROOST, HIVES PASSAGE

Fig. 8.11B Eagle Roost site, showing entrance to main *tomo* (vertical shaft) entrance for birds preserved in fossil deposit (after Millener 1984).

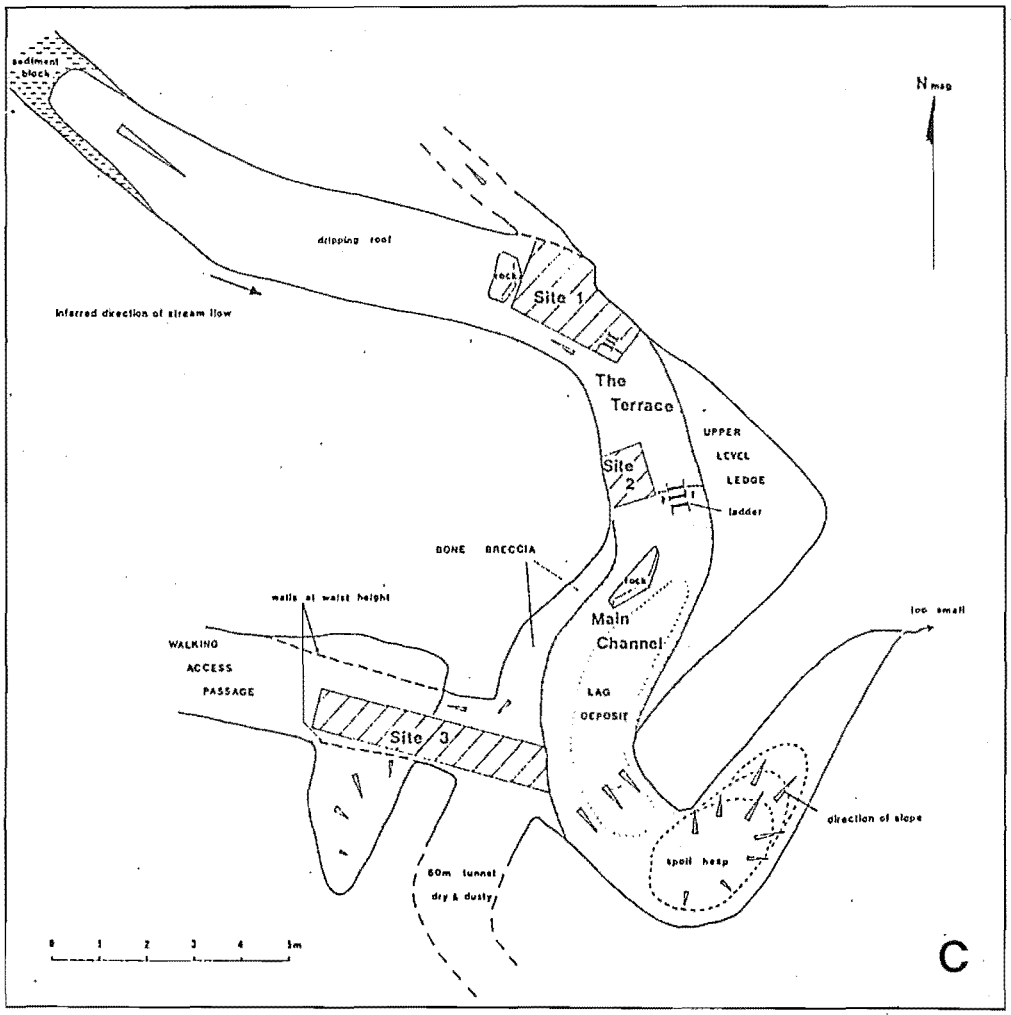

Fig. 8.11C Graveyard deposit, Honeycomb Hill, plan of excavations. After Worthy & Mildenhall (1989: fig. 2).

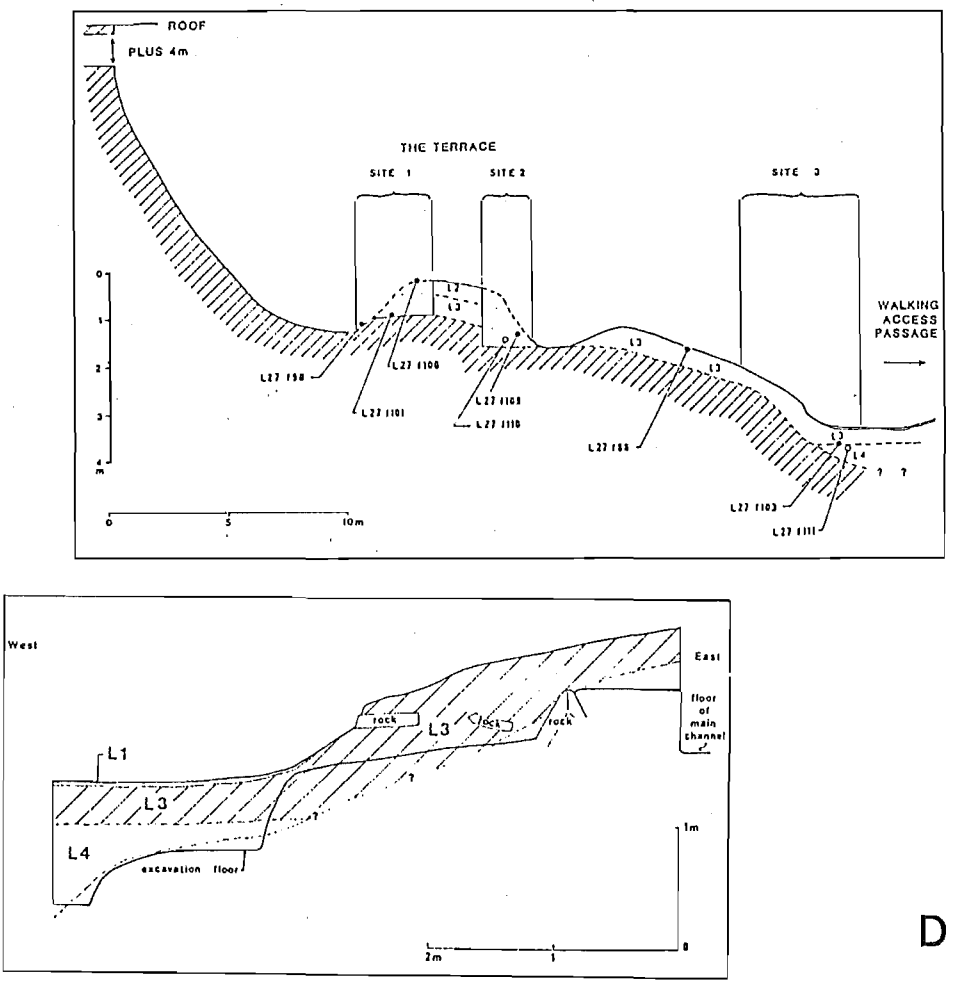

Fig. 8.11D Graveyard deposit, Honeycomb Hill, profiles of excavations. After Worthy & Mildenhall (1989: fig. 3-4).

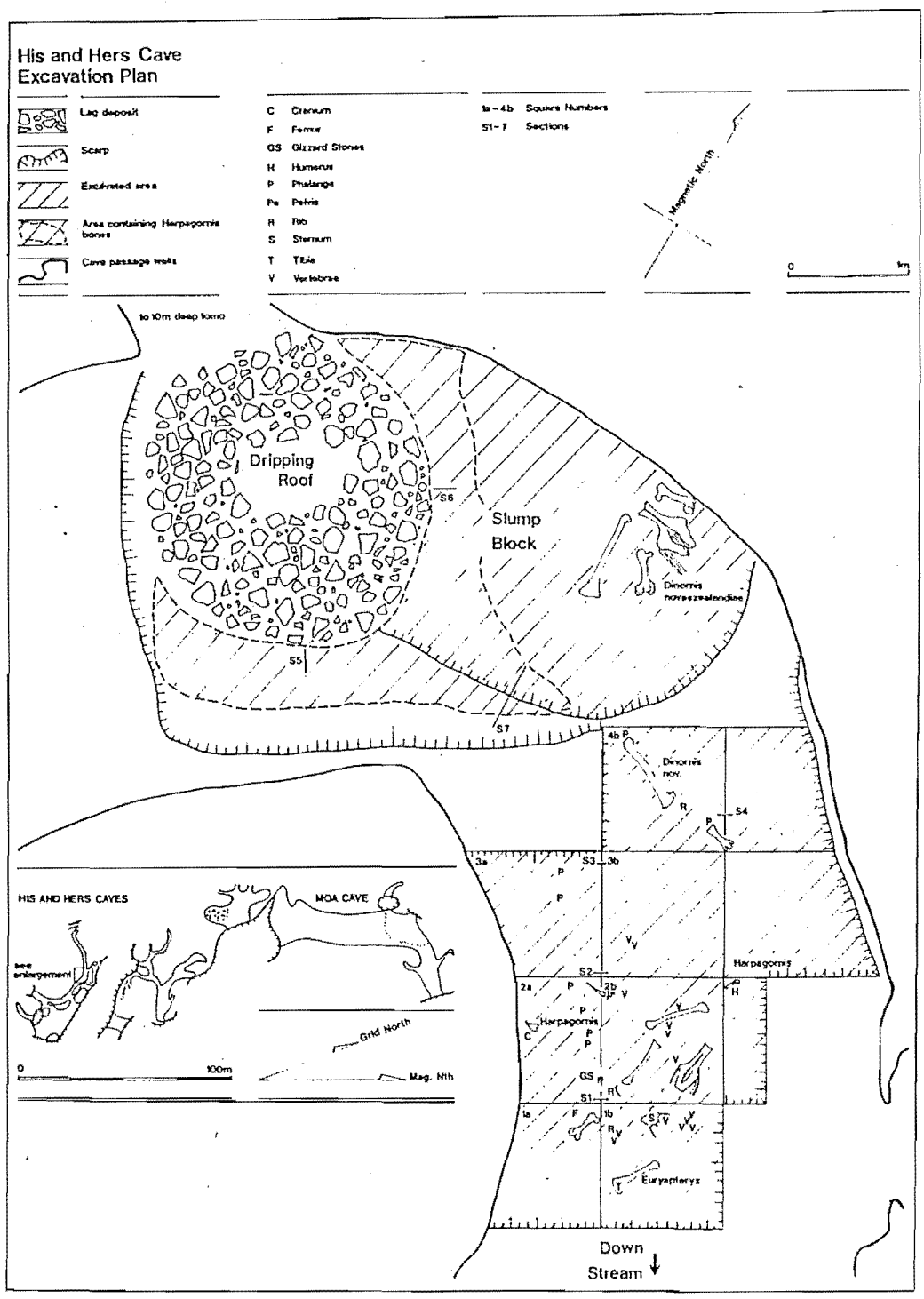

Fig. 8.11E His Cave excavation plan (after Worthy (1987).

described by Millener (1984), Worthy (1987), and Worthy & Mildenhall (1989). A full map of the cave system has not been released because of the sensitive nature and extreme importance of many of the fossil sites. Because of this, and because the sites are described in detail elsewhere, only brief comments are included here.

The deposits range in age from the Otiran glacial to late Holocene. The richest deposits date from the Pleistocene, between about 20 000 and 10 000 years BP (Worthy and Mildenhall 1989). Dates are given in Table 8.2. Later deposits contain mainly moa (Dinornithiformes) remains. Some of the deposits are stratified, and a sequence of faunas correlated with changes in the climate and vegetation in the area has been described (Worthy & Mildenhall 1989).

8.2.11.1 AR144 is to the north of the main Honeycomb Hill cave, and is connected to it by difficult passages (Worthy 1987). There is a stream in the passage, and the main fossil deposit is in stratified clays on a ledge (Worthy 1987). Worthy (1987) considered the site to be less than 14 000 years old. The main entry for birds was probably a narrow slit in the roof upstream of the deposit; it was probably a pitfall and non-return trap. The deposits were excavated by T H Worthy in 1987. One date from the site is earliest Holocene at 10 950±110 (NZA360) which suggests that deposition occurred up to and possibly beyond the Pleistocene-Holocene boundary.

Material Carpometacarpus, L, NMNZ, S 23611pt; coracoid, L, NMNZ, S 23611pt; cranium, NMNZ, S 23611pt; femur, R, NMNZ, S 23611; furcula, NMNZ, S 23611; mandible, NMNZ, S 23611; pedal ungual phalanx, NMNZ, S 23611; tibiotarsus, R, NMNZ, S 23611; ulna, L, NMNZ, S 23611; ulna, R, NMNZ, S 23611; cuneiform, NMNZ, S 23611; jugal bar, R, NMNZ, S 23611; pedal phalanx I/1, R, NMNZ, S 23611; NMNZ, S 23611; pedal phalanx III/3, L, NMNZ, S 23611; posteropterygoid, L, NMNZ, S 23611; quadratojugal + jugal, L, NMNZ, S 23611; L2, hyoid apparatus, NMNZ, S 23611; L2, manus II/2?, NMNZ, S 23611; L2, rib - fragment?, sternal a?, sternal b?, vertebral a?, vertebral b?, vertebral c?, vertebral d?, NMNZ, S 23611.

8.2.2.11.2 E entrance site is in a stream bed, in a passage below Entrance 'E' to the main Honeycomb Hill Cave. The deposits are stream-laid and probably of late Pleistocene age.

Material Humerus, L, NMNZ, S 25877.

8.2.2.11.3 Eagle Roost is below a shaft entrance (tomo) (Fig. 8.11B). Worthy (1987) considered that it acted as a trap for flying birds which entered to seek food, but could not fly up steeply enough to escape. For flightless birds, it would have been a pitfall trap. This contrasts with Millener's (1984) conclusion that the bones were deposited by a stream. The excellent preservation of many of the bones from the site, and the preponderance of small taxa, argues against its being primarily a stream-laid deposit, because of the lack of breakage and wear. The remains were found mainly on a dry ledge, in fine sediment deposited by percolation water (Worthy & Mildenhall 1989). Dates for the site range from 10 300±280 (NZA359) to 15 530±200 (NZA361).

Material Pedal phalanx II/3, R, NMNZ, S 22472.17; vertebra - dorsal c1, NMNZ, S 22472.19; 4, pygostyle, NMNZ, S 23001.1; 4, vertebra - dorsal 2, NMNZ, p S 23001.2; G, pelvis, NMNZ, S 22473.4; G, pelvis, NMNZ, S 22473.5; G, sternum, NMNZ, S 22473.2; G, sternum, NMNZ, S 22473.3; G, tarsometatarsus, R, NMNZ, S 22473.8; G, tibiotarsus, R, NMNZ, S 22473.6; G, tibiotarsus, R, NMNZ, S 22473.7; H, carpometacarpus, L, NMNZ, S 22472.7; H, carpometacarpus, R, NMNZ, S 22472.8; H, coracoid, L, NMNZ, S 22472.2; H, coracoid, R, NMNZ, S 22472.3; H, femur, L, NMNZ, S 22472.9; H, femur, R, NMNZ, S 22472.10; H, fibula, L, NMNZ, S 22472.12; H, fibula, R, NMNZ, S 22472.13; H, furcula, NMNZ, S 22472.1; H, pedal phalanx II/2, ?L, NMNZ, S 22472.15; H, pedal phalanx III/1, L, NMNZ, S 22472.16; H, radius, ?, NMNZ, S 22472.4; H, radius, ?, NMNZ, S 22472.5; H, rib a, ?, NMNZ, S 22472pt; H, rib b, ?, NMNZ, S 22472pt; H, tarsometatarsus, L, NMNZ, S 22472.14; H, tibiotarsus, L, NMNZ, S 22472.11; H, ulna, L, NMNZ, S 22472.6; H, vertebra - cervical c11, NMNZ, S 22472.22; H, vertebra - dorsal 3, NMNZ, S 22472.20; H, vertebra - dorsal 3, NMNZ, S 22472pt; H, vertebra - dorsal 4, NMNZ, S 22472.18; H, vertebra - dorsal 6 or 7, NMNZ, S 22472.21; humerus, R, NMNZ, S 25581; prefrontal, L, NMNZ, S 25580pt; prefrontal, R, NMNZ, S 22472.23; rockfall L, humerus, L, NMNZ, S 22736; Section L(a) cranium, NMNZ, S 22473.1; cranium, NMNZ, S 25580.

8.2.2.11.4 Graveyard contains one of the major deposits of fossil material in the cave system (Millener 1984, Worthy 1987). The deposit is extensive and stratified (Fig. 8.11 C, D). Eagle bones were found only in the lower layers, which are of late Pleistocene age, >20 000 to c 11 000 years BP. The sediments were stream-laid, but the flow apparently varied with time, and has resulted in differential sorting and preservation regimes so that different taxa dominate each layer. These differences are largely related to the size of the elements involved (Worthy & Mildenhall 1989). Dates for the layers in the site are that have yielded eagle material range from 20 600±450 (NZ7292) to 14 030±180 (NZ6586) years BP.

Material Carpometacarpus, R, NMNZ, S 22653pt; coracoid, L, NMNZ, S 22653pt; coracoid, R, NMNZ, S 22653pt; cranium, NMNZ, S 22712.1; tarsometatarsus, R, NMNZ, S 23073.1; tibiotarsus,

L, NMNZ, S 22653pt; 1, furcula, NMNZ, S 23720pt; 1, tarsometatarsus, L, NMNZ, S 23720pt; 1, ulna, ?, NMNZ, S 23664pt; 1/L3, scapula, L, NMNZ, S 23664pt; 3, carpometacarpus, L, NMNZ, S 23825pt; 3, cranium, NMNZ, S 23825pt; 3, femur, L, NMNZ, S 23030pt; 3, femur, R, NMNZ, S 23825pt; 3, femur, R, NMNZ, S 23825pt; 3, furcula, R, NMNZ, S 23825pt; 3, humerus, L, NMNZ, S 23030pt; 3, humerus, L, NMNZ, S 23825pt; 3, humerus, R, NMNZ, S 23825pt; 3, mandible, L, NMNZ, S 23825pt; 3, mandible, R, NMNZ, S 23825pt; 3, radius, ?, NMNZ, S 23825pt; 3, tarsometatarsus, L, NMNZ, S 23825pt; 3, tarsometatarsus, R, NMNZ, S 23825pt; 3, tibiotarsus, L, NMNZ, S 23825pt; 3, ulna, R, NMNZ, S 23030pt; 3, ulna, R, NMNZ, S 23825pt; 3, ulna, R, NMNZ, S 23825pt; 1/L3, pelvis, NMNZ, S 23664pt; lag, radius, R, NMNZ, S 23073.2; O, mandible, NMNZ, S 22765; s1, ulna, ?, NMNZ, S 23664pt; 3, humerus, L, NMNZ, S 23825pt; 3, humerus, R, NMNZ, S 23825pt; 3, tarsometatarsus, L, NMNZ, S 23825pt; 3, ulna, R, NMNZ, S 23825pt; terrace, radius, L, NMNZ, S 23051.5; terrace, radius, R, NMNZ, S 23051.4; terrace, scapula, L, NMNZ, S 23051.2; 1/L3, fibula, ?, NMNZ, S 23664pt; beyond terrace, pedal ungual phalanx II/3, R, NMNZ, S 22712.2; main passage, manus phalanx II/2, ?, NMNZ, S 23073.3; 1/L3, pedal phalanx III/1, R, NMNZ, S 23664pt; 3, cranium, NMNZ, S 23825pt; 3, pelvis, NMNZ, S 23030pt; terrace, cuneiform, L, NMNZ, S 23051.3; terrace 2, sternum, NMNZ, S 23051.1; 1/L3, carpometacarpus, L, NMNZ, S 23664pt; 1/L3, tarsometatarsus, R, NMNZ, S 23664pt; 3, cranium, NMNZ, S 23825pt.

8.2.2.11.5 His Cave (AR125) is one of a pair named His & Hers (AR124) south of the main Honeycomb Hill cave system (Fig. 8.11A). It was discovered on 30 May 1981 by P G Wood, K Rae, and P Grafton (P G Wood, pers comm). The bone deposit is in stream sediments downstream from a 10 m deep tomo, which probably acted as a pitfall and no-return trap for birds. It was excavated by T H Worthy in 1986 (Fig. 8.11E). The material had suffered stream erosion, and was fragmented, but eagle bones were the most abundant avian remains at the site (Worthy 1987). A single date of 15 900±240 years BP (NZ7321) suggests that the site is of late Pleistocene age.

Material Carpometacarpus, L, NMNZ, S23454; carpometacarpus, L, NMNZ, S 23455; carpometacarpus, R, NMNZ, S 23456; carpometacarpus, R, NMNZ, S 23457; carpometacarpus, R, NMNZ, S 23458; coracoid, L, NMNZ, S 23451; coracoid, L, NMNZ, S 23452; coracoid, L, T H Worthy collection (to NMNZ); coracoid, R, NMNZ, S 23453; coracoid, R, T H Worthy collection (to NMNZ), none; femur, L, NMNZ, S 23462; femur, L, NMNZ, S 23464; femur, L, NMNZ, S 23465; femur, R, NMNZ, S 23463; fibula, L, NMNZ, S 23476pt; fibula, R, NMNZ, S 23476pt; furcula, NMNZ, S 23450; humerus, L, NMNZ, S 23431; humerus, L, NMNZ, S 23432; humerus, L, NMNZ, S 23433; humerus, L, NMNZ, S 23459pt; humerus, L, NMNZ, S 23459pt; humerus, R, NMNZ, S23459pt; humerus, R, NMNZ, S 23459pt; mandible, NMNZ, S 23480; mandible, NMNZ, S 23480pt; pedal phalanx I/1, R, NMNZ, S 23478.3; pedal phalanx II/3, R, NMNZ, S 23478.4; pedal phalanx III/3, L, NMNZ, S 23478.1; pedal phalanx III/3, R, NMNZ, S 23478.2; pelvis, NMNZ, S 23460; pelvis, NMNZ, S 23461; radius?, NMNZ, S 23445; radius, L, NMNZ, S 23443; radius, R, NMNZ, S 23440; radius, R, NMNZ, S 23441; radius, R, NMNZ, S 23442; radius, R, NMNZ, S 23444; scapula, L, NMNZ, S 23448; scapula, L, NMNZ, S 23449; scapula, R, NMNZ, S 23446; scapula, R, NMNZ, S 23447; tarsometatarsus, L, NMNZ, S 23473; tarsometatarsus, L, NMNZ, S 23474; tarsometatarsus, L, NMNZ, S23475; tarsometatarsus, R, NMNZ, S 23472; tarsometatarsus, R, NMNZ, S23477; tibiotarsus, L, NMNZ, S 23467; tibiotarsus, L, NMNZ, S 23470; tibiotarsus, R, NMNZ, S 23466; tibiotarsus, R, NMNZ, S 23468; tibiotarsus, R, NMNZ, S 23469; tibiotarsus, R, NMNZ, S 23471; ulna, L, NMNZ, S 23435; ulna, L, NMNZ,

S 23439; ulna, R, NMNZ, S 23434; ulna, R, NMNZ, S 23436; ulna, R, NMNZ, S 23437; ulna, R, NMNZ, S 23438; vertebra - dorsal, T H Worthy collection (to NMNZ), none; Sq2a, cranium, NMNZ, S 23479.

8.2.2.11.6 Hives Extension site is a stream deposit west of Eagle Roost and separated from it by a barrier that precludes the deposits from sharing the same source (T H Worthy, pers. comm. 1990) (Fig. 8.11B). The age of the deposit, which occupies a very small area, is likely to be similar to that of Eagle Roost, i.e. late Pleistocene to early Holocene. Material from this site was collected during the 1980 Canterbury Museum inspection.

Material Carpometacarpus, L, NMNZ, S 25582; humerus, R, CM, AV 36396; tarsometatarsus, R, CM, AV 36397; ulna, L, CM, AV 36405.

[Unit Hole (AR 126) is on the left bank of the Oparara River, about 4 km south of the Honeycomb system. It was discovered on 27 October 1980 by P G Wood and a party of Venturer Scouts. A slippery grass slope occurs above the entrance, and would have enhanced its effectiveness in trapping moa, of which the remains of four were noted (P G Wood, pers comm), if the topography of the site had not changed. As the material was found on the surface, substantial change since the trapping events is unlikely. The age of the deposits is unknown.

Material Humerus, L, CM, AV 36008pt; humerus, R, CM, AV 36008pt; identified by R J Scarlett 1980; reidentified as *Cnemiornis calcitrans* by RNH.]

8.2.2.12 Hunterville (Fig. 8.12)

NZMS260 S22/296364 39°57′00″S 175°34′15″E.

Bones exposed in a railway cutting during construction of the North Island Main Trunk Railway near Hunterville in 1896? were collected by S H Drew (Drew 1896). This is the type locality for *Cnemiornis gracilis* and is probably of Pleistocene age (Millener 1981; Worthy & Mildenhall 1989). No other information is available about the site.

Material None seen (It may be in Wanganui Museum, but enquiries elicited no response.)

8.2.2.13 Kakanui Beach (Fig. 8.13)

NZMS260 J42/450560 45°11′20″S 170°54′10″E.

According to the entry in the Canterbury Museum catalogue, eagle bones were "washed from [a] bank by high tides [in] October 1974". They were "derived from [a] blue pug swamp". I did not locate the site during a visit to the area in December 1988. The Kakanui River runs out to the coast in a meander, with a long bar extending from north to south. The banks of the stream near its mouth have a blue clay layer, but it was not possible to identify the area washed out in 1974. Erosion at the north end of the spit is exposing a Polynesian occupation layer containing fish bones, shell, and charcoal.

The site probably represents a Holocene swamp deposit being eroded by recent coastal retreat, which has been rapid in this area (Anderson 1990, Gibb 1983).

Material Humerus, L, CM, AV 29361pt; tarsometatarsus, L, CM, AV 29361pt.

8.2.2.14 Kapua (Fig. 8.14)

NZMS260 J40/509011 44°46′55″S 170°59′20″E.

This site was in the bed of a pond, which occupied the lowest part of a basin filled with lacustrine sediments. The pond was near the outlet of the former lake, from which a stream flowed through Waimate Gorge. It was drained in September 1894, and moa bones were discovered during the sinking of a well. Bones were not found in the drain, which was about 2.1 m deep, but were "in patches" to either side (Hutton 1896: 628). The site excavated for Hutton by the Canterbury Museum taxidermist, W Sparkes, was to the east of the "Government drain".

The excavation extended over about 9 x 6 m, and according to Hutton (1896), the section was [metric conversions]:

[1.2 m] pale yellow clay, soft and wet in places; no bones

[0.4 m] black sandy clay; few moa bones

[1.2-1.5 m] tough blue clay; full of moa bones; the clay extended below the bone layer. A few small sticks were found, but no large pieces of wood. Few bones of birds other than moas were found.

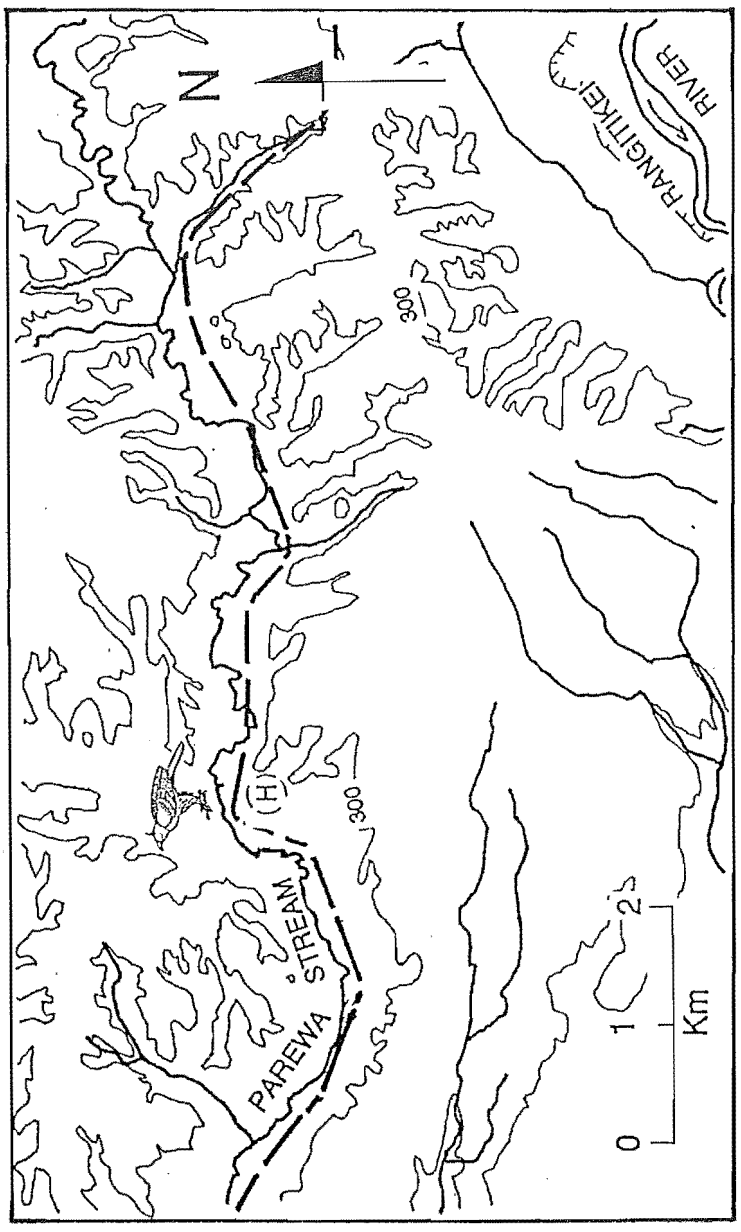

Fig. 8.12 General location of Hunterville site, Wanganui- Rangitikei area, North Island, showing topography and drainage pattern in immediate area. Site was described as being in a cutting for the North Island Main Trunk Railway (shown by long dashed line), near Hunterville (H).

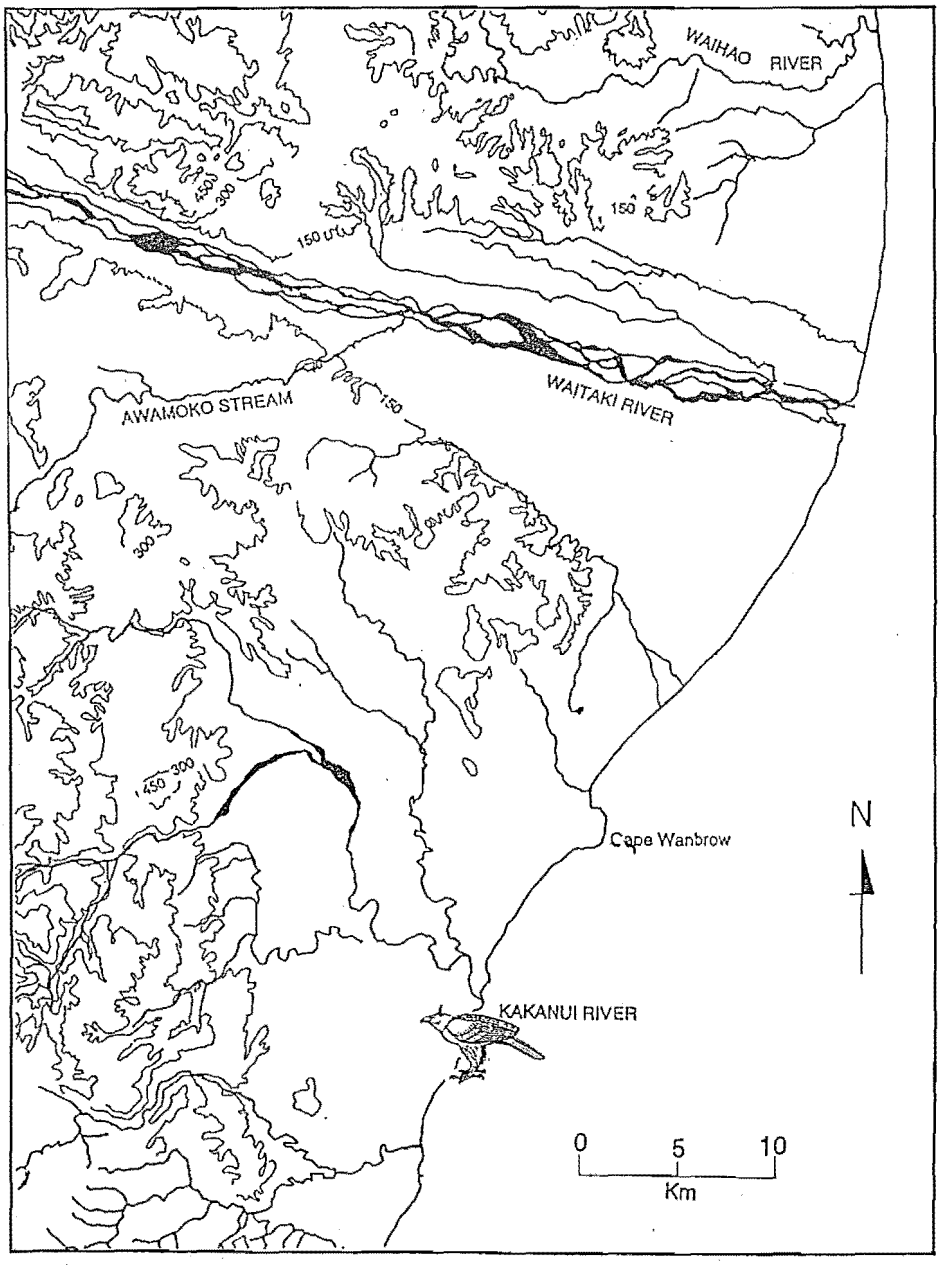

Fig. 8.13 General location of Kakanui Beach site, showing topography and drainage pattern in immediate area. Site was in river flats eroded by storm seas.

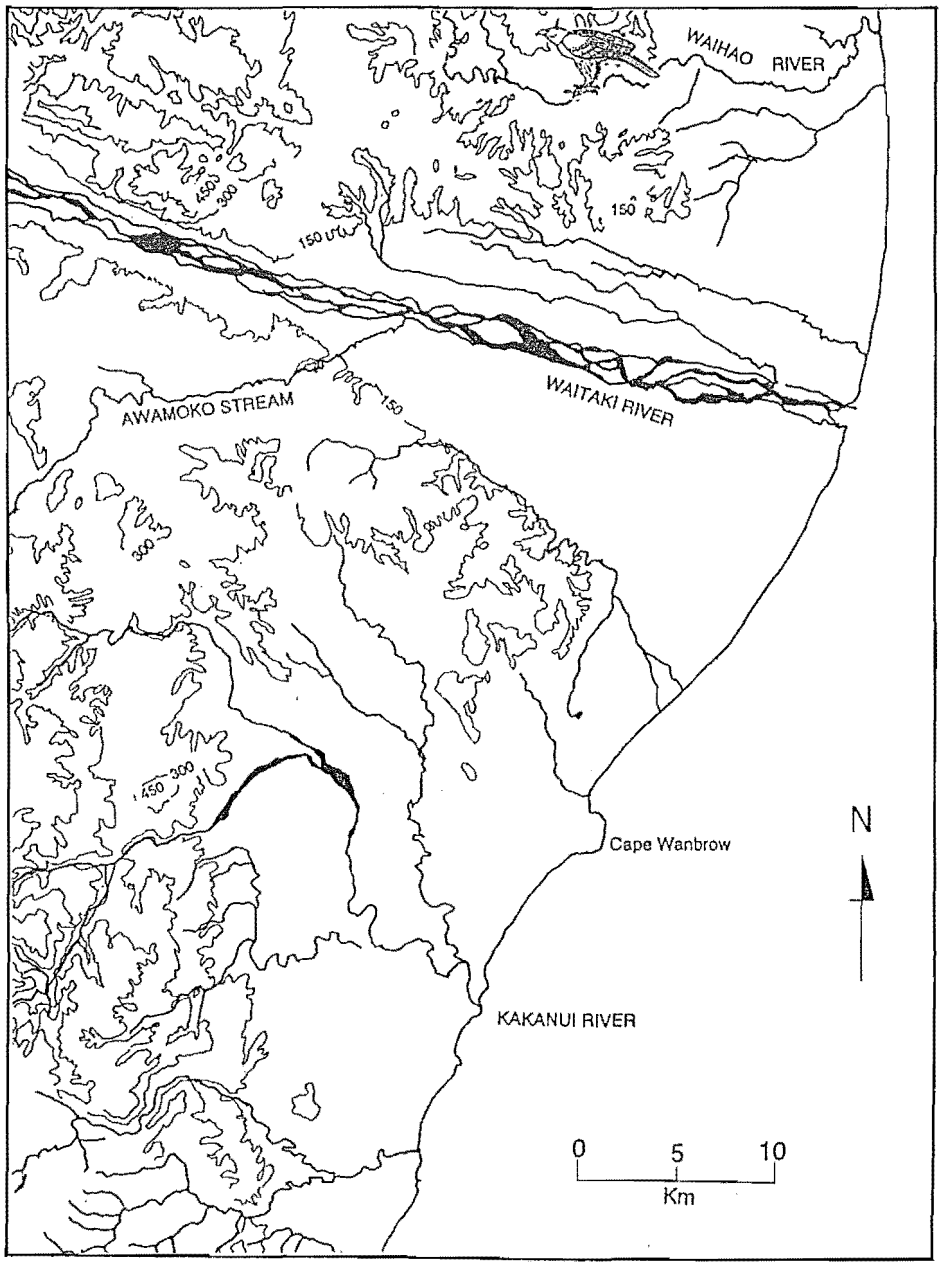

Fig. 8.14 Kapua site, near Waimate, North Otago, showing topography and drainage pattern in immediate area. Site was on bank of drain cut at entrance to Waimate Gorge.

No dates are available, but the site was probably early to mid Holocene, from the stratigraphy.

Material Tibiotarsus, R, CM, AV 5322.

8.2.2.15 Kings Cave (Fig. 8.15)

NZMS260 J38/402511 44°19′30″S 170°52′15″E.

This cave site was described briefly by Chapman (1985) and by Worthy (1988). Chapman suggested that the source of material in the deposit was a now-closed entrance from a sinkhole beyond the present upstream end of the cave. Most of the material is fragmentary, and there are no associated skeletons. Haast's eagle is represented by three small bones, which could have been washed in with bones of smaller birds; the remainder of the animal was probably too large to pass through the sinkhole entrance. Worthy (1988) suggested that the deposit was possibly several thousand years older than that at Castle Rocks, because many bones were in a sediment layer which was continuous beneath a later rockfall. The ultimate source for all the material was probably a pitfall or no-return trap sinkhole.

Material Carpometacarpus, R, CM, AV 22481; pedal phalanx, L4/2, L, CM, AV 22892pt; vertebra, CM, AV 24783pt.

8.2.2.16 Marfells Beach and Lake Grassmere sandspit (Fig. 8.16)

NZMS260 P29/095421 41°43′25″S 174°11′40″E.

This general site contains an unknown number of sites where most material, both natural and with cultural association, has been surface collected from blow-outs in the dunes. The provenance of most bones is given as simply dunes or sand-hills at Lake Grassmere or Marfells Beach, although one is stated to be from the Te Hau property, which occupies part of the dune and beach complex. Each bone from the area could well represent a separate individual and site. J R Eyles (pers. comm. August 1990) recalled finding many bones from a single skeleton when visiting the area with a Canterbury Museum party in the 1940s, but they were put in an old oven at the then-new salt works and were not retrieved. As Scarlett (1979) pointed out, there is no evidence that any of the bones from the Marfells site were associated with cultural layers.

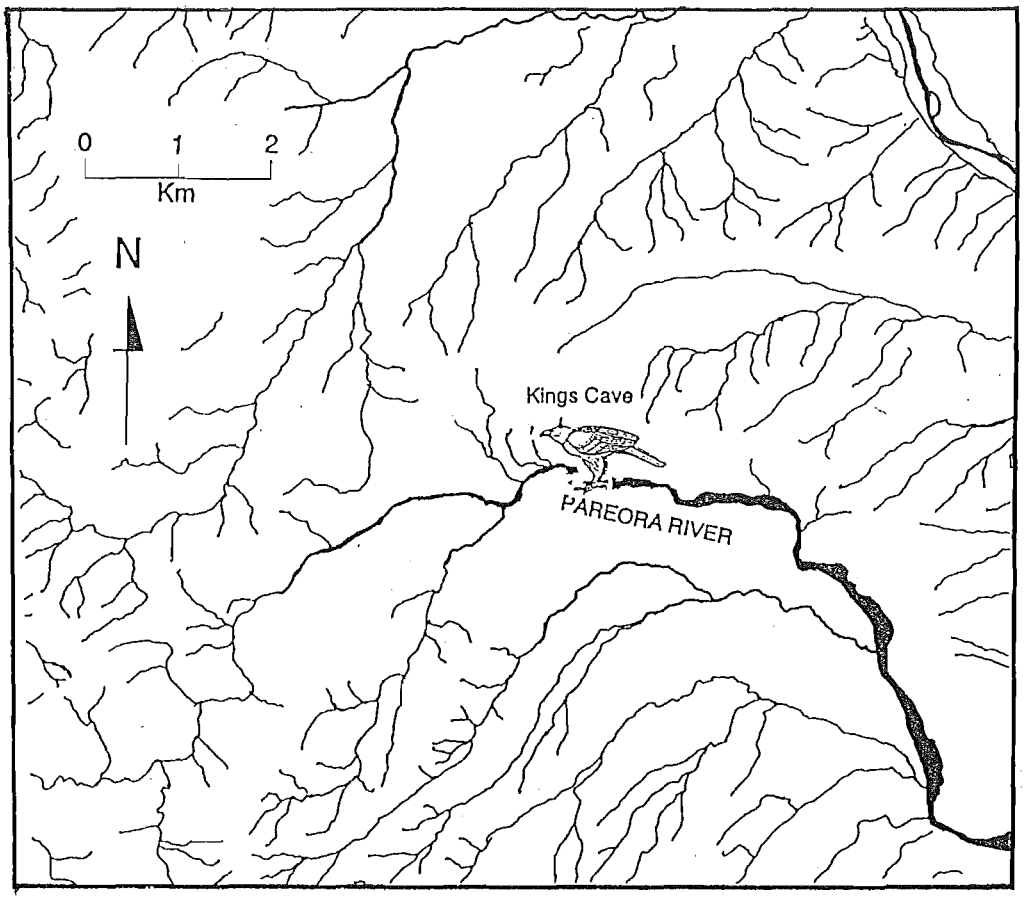

Fig. 8.15 Kings Cave site, near Cave, South Canterbury, showing topography and drainage pattern in immediate area.

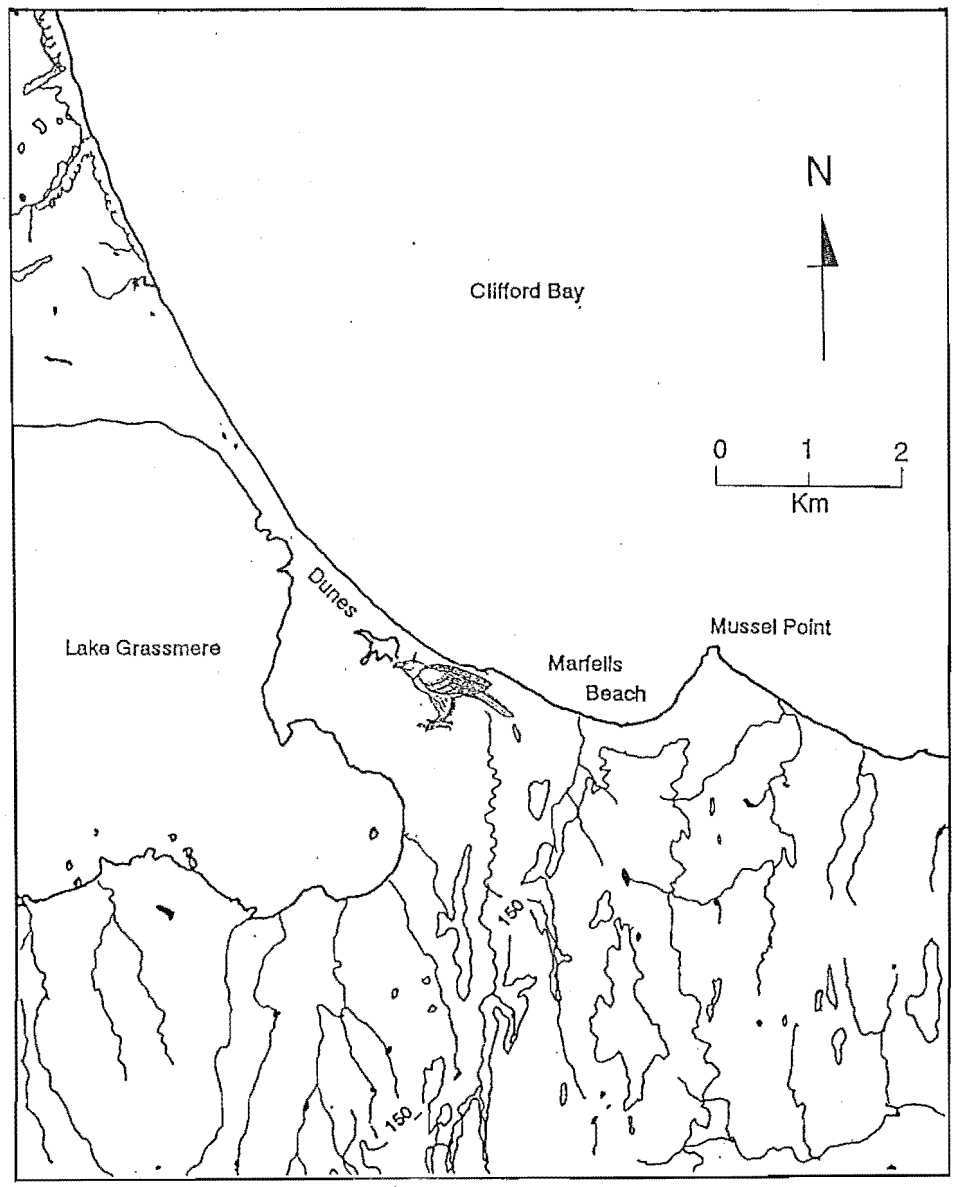

Fig. 8.12 Marfells Beach site, northeast coast of Marlborough, showing topography and drainage pattern in immediate area. Eagle material was collected from different "blow-outs" in the dunes before the area was stabilised with marram grass. None of the sub-sites was accurately located by the collector at the time of collection.

The dunes at the site are probably younger than about 6 000 years if the inner shore of Lake Grassmere represents the sea level indicated by the dune line on the Wairau Plain in the next valley north (Brown 1981). Present sea level was established by about 6 500 years BP (Gibb 1983).

Material Carpometacarpus, L, CM, AV 11163; coracoid, L, CM, AV 13014; mandible, CM, AV 12152; pedal phalanx, ?, CM, AV 33768; pedal ungual phalanx, CM, AV 11486; pedal ungual phalanx, CM, AV 11515; pedal ungual phalanx, CM, AV 11700; pedal ungual phalanx, CM, AV 12153; pedal ungual phalanx, CM, AV 22268pt; tarsometatarsus, L, CM, AV 12263; tibiotarsus, L, CM, AV 11041; femur, R, CM, AV 9651; pedal phalanx?, CM, AV 12555; pedal phalanx II/3, R, CM, AV 14254; vertebra - dorsal, CM, AV 16329; Te Hau, tarsometatarsus, L, CM, AV 16221; pedal ungual phalanx, CM, AV 22268pt.

8.2.2.17 Motunau (Fig. 8.17)

NZMS260 N34/194005 43°00′30″S 173°30′30″E.

Alexander McKay investigated a deposit of moa bones near the Motunau River mouth for Dr J Hector of the New Zealand Geological Survey. The deposit had been reported to Hector by the landowner, Mr W Robinson. A winter flood in 1881, exposed the deposit in the banks of a creek forming the boundary between Robinson's property, and one owned by Mr W Arkle. The stream was north of Boundary Creek, which appears on modern maps, and was one of the small streams that arise on the coastal plain, then cut down through deep gravels and then rock. The short deep gorges end at the coastal cliffs. McKay (1882) described the stratigraphy at the site. He pointed out that the deposit exposed by the stream extended north and south of the stream bed, and consisted of a layer of "peaty lignite" with sands and clays, and tree trunks, which occurred between six and nine metres (20-30 ft) above the base of thick gravels and silts. In an excavation covering "about 30 square feet [c 1 m^2]" in a field on the north side of the stream, beside the start of the gorge, the stratigraphy was, in metric equivalents:

[1.52-1.83 m "sandy loam", with tree stumps in growth position at the base, these not showing near the surface

[0.61-0.92 m] sand, with patches of gravel

? variable, from sand to plastic clay, over

[0.30-0.61 m] thickly packed bones in a soft tough clay

? "well rounded gravel" of unknown thickness at this point.

In a further description of the site, McKay (1882: 75-76) noted that the deposit was extensive and that the thickest part extended northeast from the north bank of the creek. The bone bed was thinner in the southern bank and lacked bones upstream from the main deposit, being there a "peaty lignite". Across the channel, however, at the base of a low cliff being cut back by the stream, there were more bones, and they were more crushed and fragile than those found in the clay downstream. The bones here increased from occasional elements to a bed 200 mm thick, with 200 mm of overlying peat. McKay (1882) also pointed out (p. 77) that the thickness of the gravels above the bone bed was "indefinite" "having been unequally denuded in different localities".

McKay (1882) suggested that the gravels near Motunau might be contemporaneous with the lower gravels at Glenmark Creek and the Omihi Valley (where Haast had found peat lenses with bone), and those near Gore Bay, where McKay had also found moa bone and eggshell. Regardless of whether there is any relationship with the Glenmark series, deposition at the Motunau site is clearly not the result of any ponding or swamp on the present stream. The lignite and tree trunks associated with the bones suggest a forest, or at least woodland, environment, possibly around a pond or small lake. This vegetation was replaced some time later by another forest, judging by the *in situ* trunks 60-90 cm above the bone bed. This second forest also became buried, apparently while standing, by an unknown amount of sediment.

McKay (1882) also suggested that there was some separation of the various elements of the moa carcases preserved in the deposit. Tarsometatarsi were most common at the eastern end, with tibiotarsi in the centre, and femora at the western end. At the thickest part of the bed, crushed and decomposed pelves were on top of the other bones. Smaller bones, such as vertebrae and phalanges, were scattered through the main bed, and were also present in clay overlying the main bed to the west. There, a tarsometatarsus was found with the phalanges in position; the tarsometatarsus was horizontal in the clay and the phalanges were aligned vertically.

Most of the non-moa bones were of Haast's eagle. All the wing and leg bones were found with their long axes vertical (McKay 1882: 76). A skull was

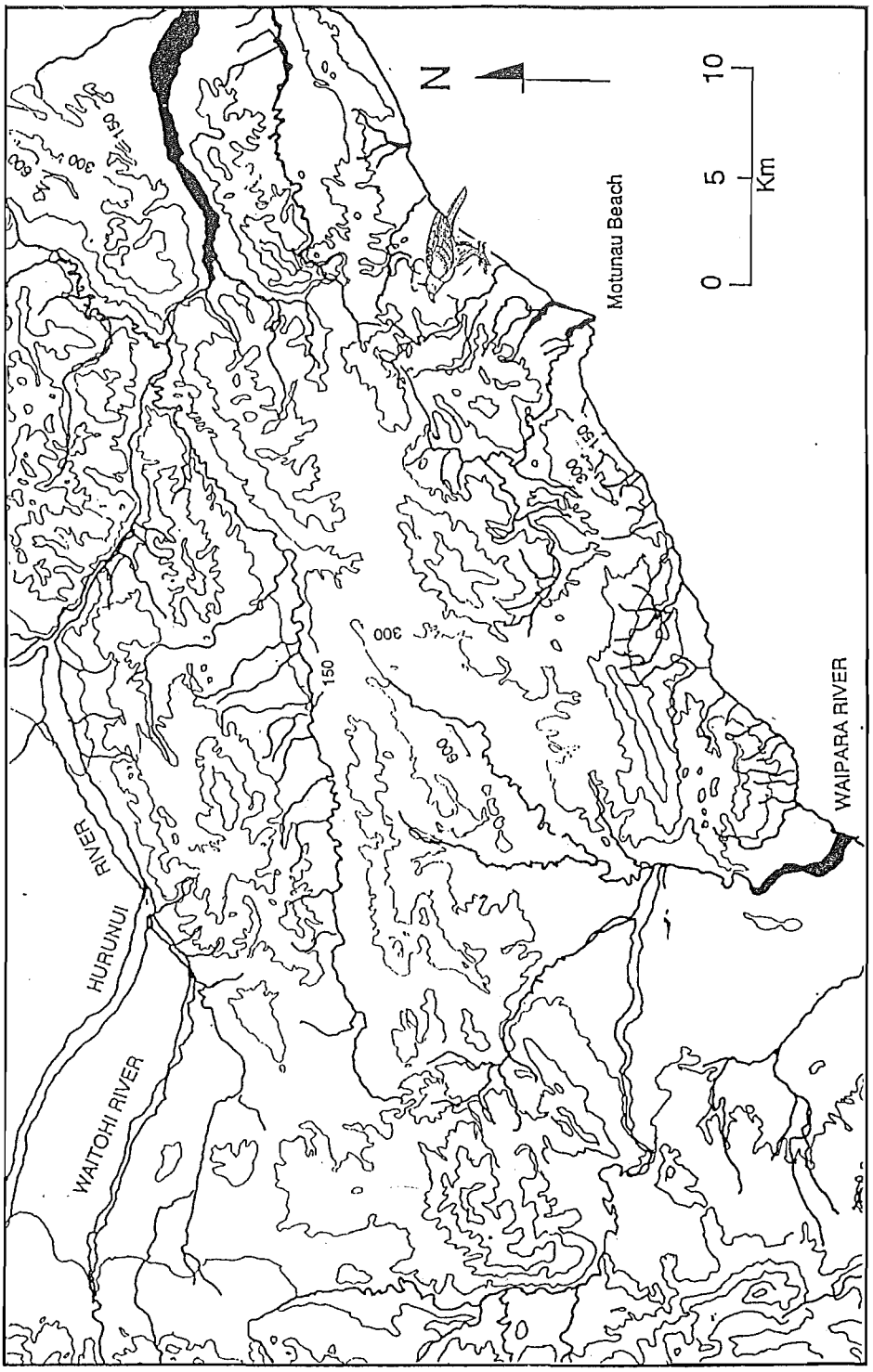

Fig. 8.17 Motunau site, north of the Motunau River Mouth, North Canterbury, showing topography and drainage pattern in immediate area. Site was in bed of one of the small streams arising in the raised coastal plain, north of Boundary Creek.

protected by two large moa bones.

The site was either visited again by Forbes in the late 1880s or early 1890s, or else Forbes removed or was given some of McKay's collection, because several elements labelled "Motanau" are now in the Forbes collection in BMNH (see below). The "skull" referred to by McKay has not been identified in collections. An albatross cranium in NMNZ, labelled as *Harpagornis moorei*, may be from Motunau, or alternatively, the skull in BMNH apparently from Enfield may be the Motunau specimen. The comment of Hamilton (1893) is the last mention of its existence.

No radioisotope date is available for the site.

Material Carpometacarpus, L, NMNZ, DM 2143pt; femur, R, NMNZ, DM 2143pt; humerus, L, NMNZ, DM 2143pt; metatarsal 1, L, BMNH, A 1512pt; pedal phalanx ?, ?, BMNH, A 1512pt; pedal phalanx ?, ?, BMNH, A 1512pt; tarsometatarsus, R, BMNH, 93.1.30.21; tarsometatarsus, R, NMNZ, DM 2143pt; tibiotarsus, L, NMNZ, DM 2143pt.

8.2.2.18 Mount Owen (SO 209) (Fig. 8.18 A-G)

NZMS260 M28/715615 41°33′15″S 172°32′15″E.

This very important site is also one of the most unusual. Elements of the skeleton were found on, in, and near a small rockfall at the bottom of a narrow-mouthed sinkhole (NZ Speleological Soc. Ref SO 209) on an exposed ridge near the summit of Mt Owen, a dissected and glaciated marble massif rising to about 1875 m. The entrance to the sinkhole is about 1 m in diameter (Fig. 8.18E) and leads into a vertical shaft about 15 m deep, with two chambers at the bottom. The ridge is narrow enough for a bird standing near the entrance to the sinkhole to be able to see out across two large subalpine basins.

In early January 1990, D Smith, a student from Waikato University, found bones while investigating possible entrances to the Bulmer cave system, which lies within the Mount Owen massif. Most of the bones of the skeleton of one individual were found together in positions that appeared to correspond to those where the various body parts lay as they twisted and distorted after death, although they were not articulated. Several bones, including the skull, sternum, and some wing bones were removed. These were shown to T H Worthy in Nelson some days later, and the remaining material searched for systematically

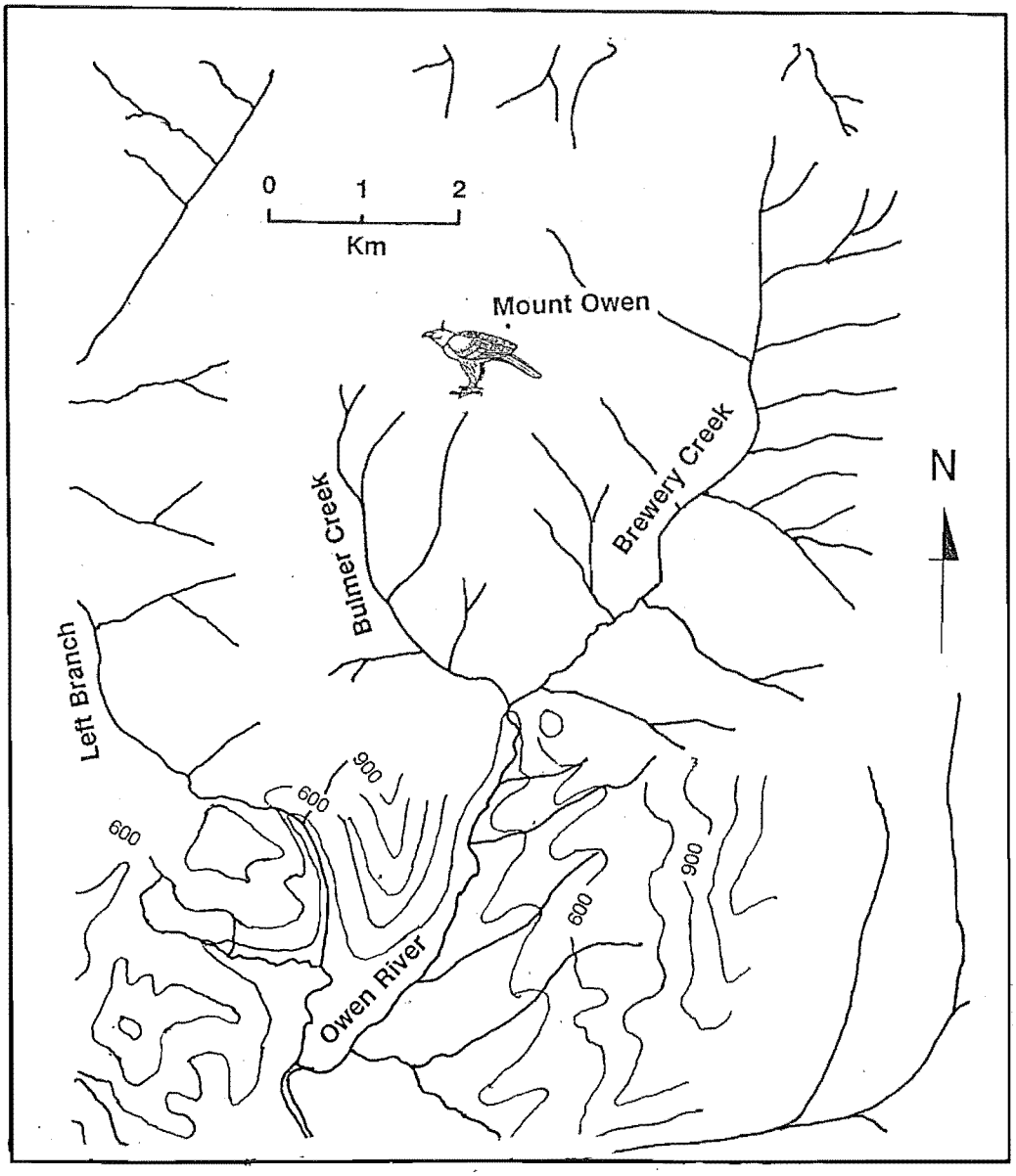

Fig. 8.18 (A-G) Mount Owen site, southwestern Nelson: A, showing location of area, and topography and drainage pattern in immediate area.

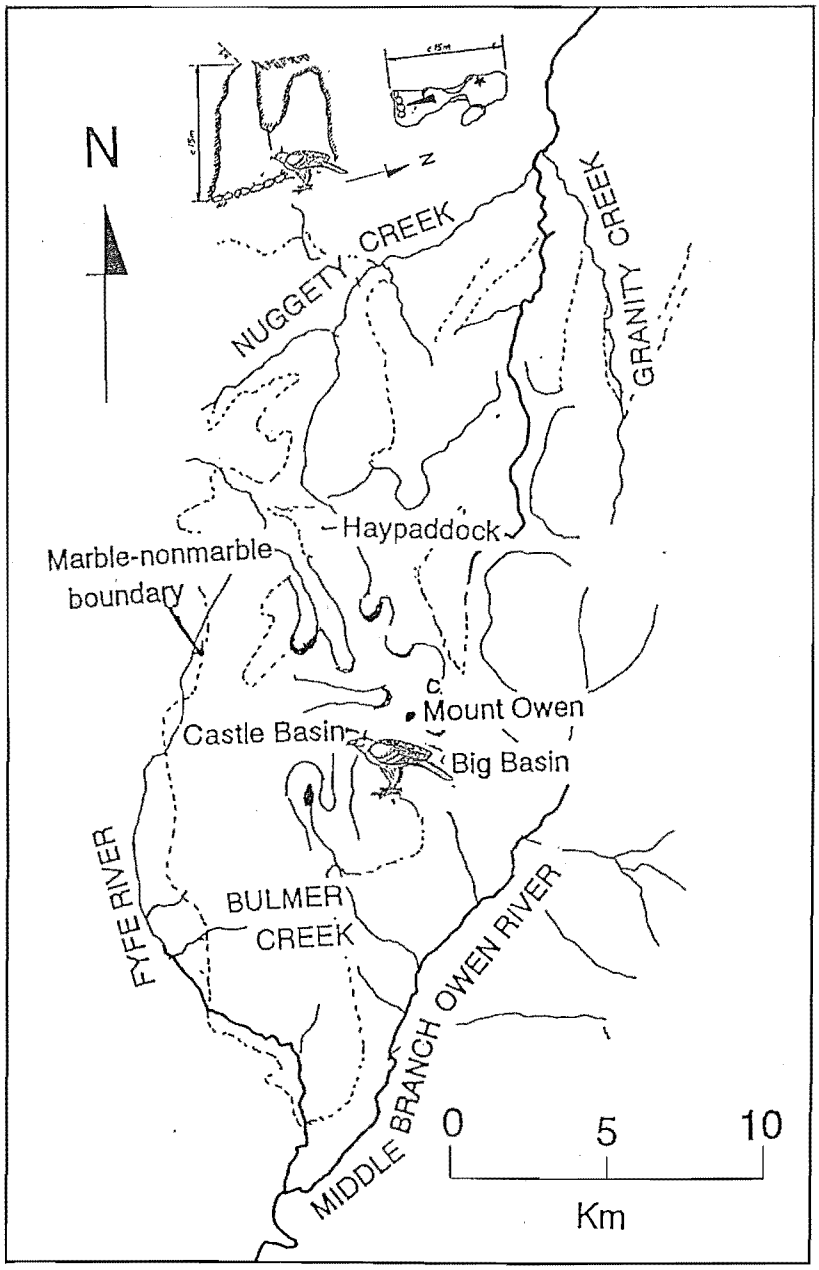

Fig. 8.18B Location of cave SO 209, and distribution of karst and glacial features on Mount Owen (after Williams, in Soons 1982: fig. 6.1).

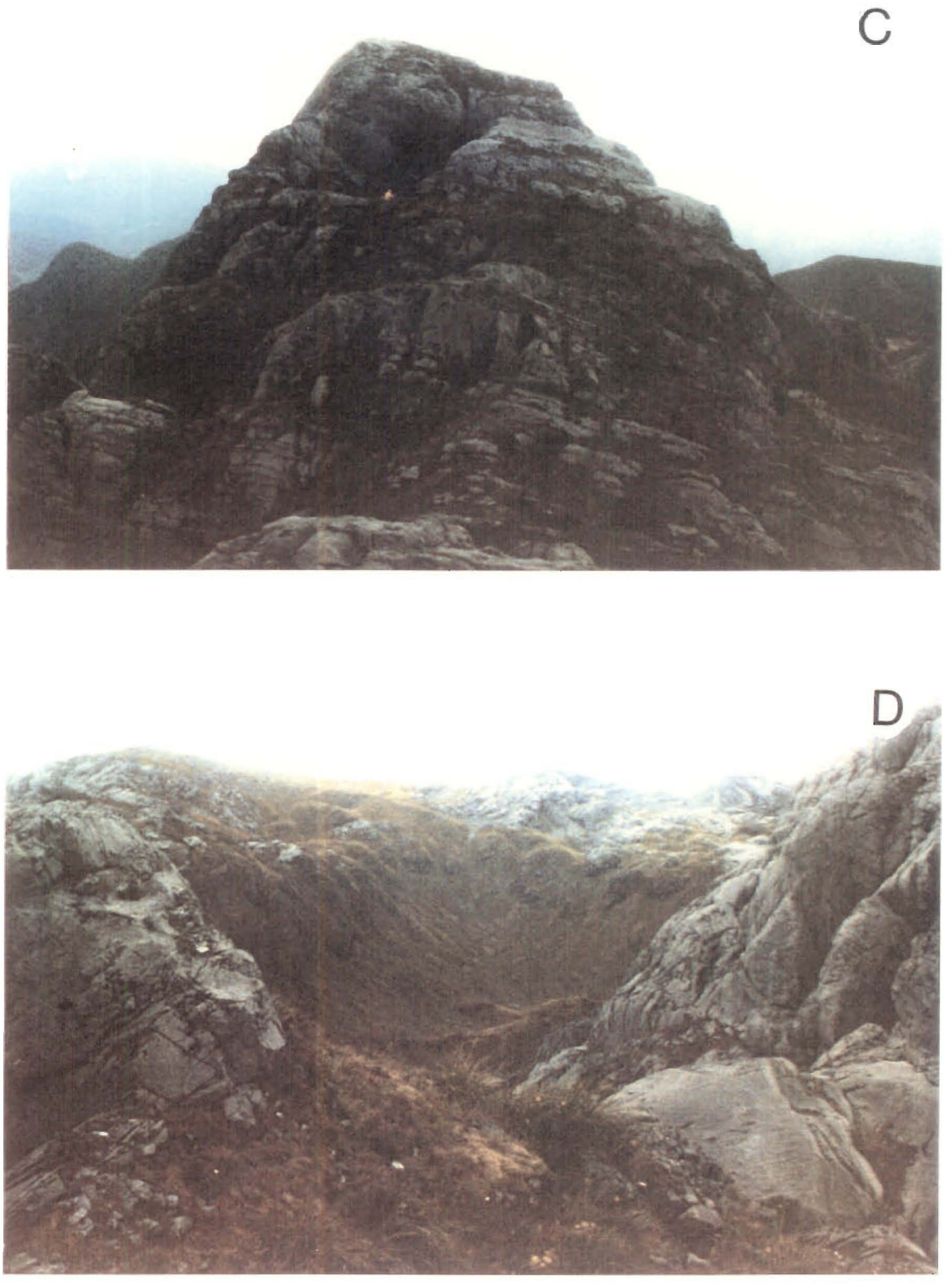

Fig. 8.18 (C, D) **C**, View south along leading ridge from Mount Owen; entrance to cave SO 209 is 18 mm to right of and below figure in yellow parka; **D**, view of Castle Basin, a glacial cirque cut into karst terrain southwest of summit of Mount Owen, from entrance to cave SO 209. (Photographs on Mount Owen, courtesy T H Worthy).

Fig. 8.18 (E, F) **E**, Entrance to cave SO 209; entrance is c 1 m wide; **F**, eagle bones from single individual (NMNZ S 27773) *in situ* on rockfall in second chamber of cave SO 209, lens cap is c 50 mm dia; bones as found, femur in foreground moved from original position. (Photographs on Mount Owen, courtesy T H Worthy).

Fig. 8.18G Material removed by D Smith at time of discovery, showing range of elements normally perceived as interesting by an observant explorer.

and removed on 14 January 1990 by a party consisting of Smith, Worthy, and P R Millener of the National Museum. The pelvis was found away from most of the remains, on the other side of the rock pile, in the second chamber, where it had probably been carried by a weka (*Gallirallus australis*), whose remains were also found in the cave. A fibula from the eagle was dated at 2160±110 years BP (NZA 905, P R Millener, pers, comm.).

Material All NMNZ, S 27773: Mandible; carpometacarpus, L, R; coracoid, L, R; cranium; femur, L, R; fibula, L, R; humerus, L, R; hyoid apparatus (7 parts); manus II/1, L, R; manus II/2, R; manus III/1, L, R; metatarsal 1, L, R; pedal phalanx I/1, L, R; pedal phalanx I/2, L, R; pedal phalanx II/1, L, R; pedal phalanx II/2, L, R; pedal phalanx II/3, L, R; pedal phalanx III/1, L, R; pedal phalanx III/2, L, R; pedal phalanx III/3, L, R; pedal phalanx III/4, L, R; pedal phalanx IV/1, L, R; pedal phalanx IV/2, L, R; pedal phalanx IV/3, L, R; pedal phalanx IV/4, L, R; pedal phalanx IV/5, L, R; pelvis; pollex, L, R; posteropterygoid, L, R; prefrontal, L, R; pygostyle; quadrate, L, R; quadratojugal, L, R; radiale, L, R; radius, L, R; rib - sternal 1, L, R; 2, L, 2, R; 3, L, R; 4, L, vertebral 1, L, R; 2, L, R; 3, L, R; 4, L, R; 5, L, R; 6, L, R; 7, L, R; 8, L, R; scapula, L, R; scleral ossicles (3), ?; sternum; superciliary, L, R; tarsometatarsus, L, R; tibiotarsus, L, R; ulna, L, R; ulnare, L, R; vertebra - caudal 1, 2, 3, 4, 5, 6; cervical 1 (atlas), 2 (axis), 3, 4, 5, 6, 7, 8, 9, 10, 11; dorsal 1, 2, 3, 4, 5, 6, 7.

8.2.2.19 Ngapara (Fig. 8.19 A, B)

NZMS260 J41/785308 44°58′50″S 170°43′40″E.

Hamilton (1904) investigated this locality in 1903. Other collections were made into the 1930s, but nothing has been published about them. The material was found in sediments where solution fissures in limestone had led to lateral collapse of limestone slabs, exposing the floors of former pitfall or non-return traps (Fig. 8.19B). Bones have been found at several sites within the locality, but the exact positions of these sites have not been recorded. The area is rolling downland, drained by small tributaries of the lower Waitaki River. The map reference is for a farm in Paradise Valley, where the terrain appears to match Hamilton's (1904) description.

No dates are available for the site, but it likely to be of Holocene age, because of the state of preservation of the exposed bones, and the lack of erosion of the site itself.

Material Carpometacarpus, L, OMNZ, C 32.81; coracoid, L, OMNZ, C 32.82; pedal phalanx II/1, R, OMNZ, C 03.61; pedal phalanx, ?, OMNZ, C 03.61; pedal phalanx II/2, ?, OMNZ, C 23.27; pedal phalanx II/2, R, OMNZ, C 03.61; pedal phalanx II/2 or II/3, ?, OMNZ, C 23.27; radius, L, OMNZ, C 03.61pt; sternum, OMNZ, C 03.61pt; tarsometatarsus, L, OMNZ, C 32.83pt;

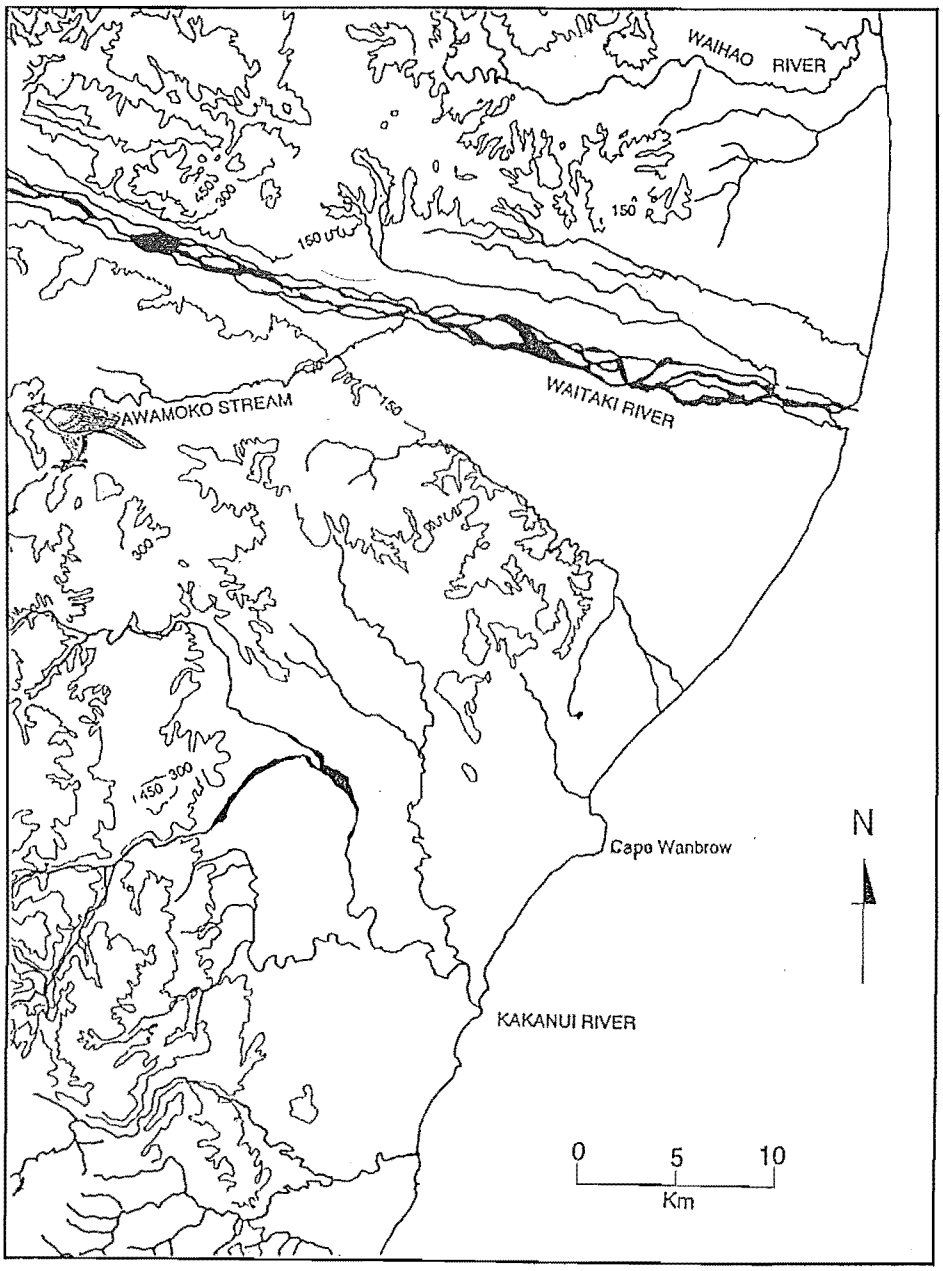

Fig. 8.19 (A, B) Ngapara site, Waitaki Valley, North Otago: A, Approximate location of site, showing topography and drainage pattern in immediate area.

DIAGRAM OF THE MODE OF OCCURRENCE OF THE BIRD-BONES AT NGAPARA.

A. Limestone. B. Sands and clays.

Fig. 8.19B Detail of Ngapara site as excavated/collected in 1903, from Hamilton (1904: text figure, p. 476.).

tarsometatarsus, R, OMNZ, C, 03.60; tarsometatarsus, R, OMNZ, C 32.83pt; ?, coracoid, L, OMNZ, unnumbered; ?, humerus, R, OMNZ, A1 C 23.29?; ?, quadrate, OMNZ, C 03.61, ?; ?, scapula, R, OMNZ, A/4 C 23.29?; ?, sternum, R, OMNZ, A/3 C 23.29?.

8.2.2.20 Oamaru/Wanbrow (Fig. 8.20A)

NZMS260 J41/503627 45°07′35″S 170°58′00″E.

Situated on the southern side of Cape Wanbrow, at the mouth of Shirley Creek, this site is referred to as Shirley Creek by B McCulloch (*in lit.*), and the bones probably come from the same individual as those listed below under that subsite below (T H Worthy pers. comm. 1990). The site was similar to Old Rifle Butts (see below), and is probably in or near S136/f1213 described by Grant-Mackie & Scarlett (1973). This was 1.5-2.0 m of weathered yellow sand and clay on 0.3-1.0 m of unfossiliferous gravel resting on an Upper Eocene basement. Continuing coastal erosion has exposed new material at irregular intervals, before destroying the deposit. It was also a marine deposit of at least last interglacial age (see **Old Rifle Butts** below for comments on dating).

Material Femur, L, AUNZ, AU 9723; femur, R, AUNZ, AU 9723pt; ulna, R, AUNZ, AU 9723; vertebra - cervical, AUNZ, AU 9723pt.

"**Shirley Creek**" Collected, Bruce McCulloch, 1979 (McCulloch 1979, in lit.)

Material Coracoid, NOM; radius, NOM; tarsometatarsus, NOM; tibiotarsus, NOM; ulna, NOM; tarsometatarsus, NOM.

8.2.2.21 Old Rifle Butts (Fig. 8.21 A-D)

NZGS S136/f1212 NZMS260 J41/501627 45°07′35″S 170°58′00″E.

This was a lens of sand and carbonaceous silt within a dune sand layer in the Hillgrove Formation (Oturian Interglacial) which rests unconformably on the Miocene Rifle Butts Formation on the southern side of Cape Wanbrow. The site was a lens of pebbly sand 45 cm thick representing an "aquatic deposit" within a stratum of dune sands. The lens contained a "rich avifauna and rarer molluscs" (Grant-Mackie & Scarlett 1973). Other thin lenses above the major fossiliferous layer, thought to be of similar origin, were taken to represent "the quiet environment of small, almost enclosed, possibly brackish-water, estuaries or lagoons. The section is overlain by several metres of loess, presumably from

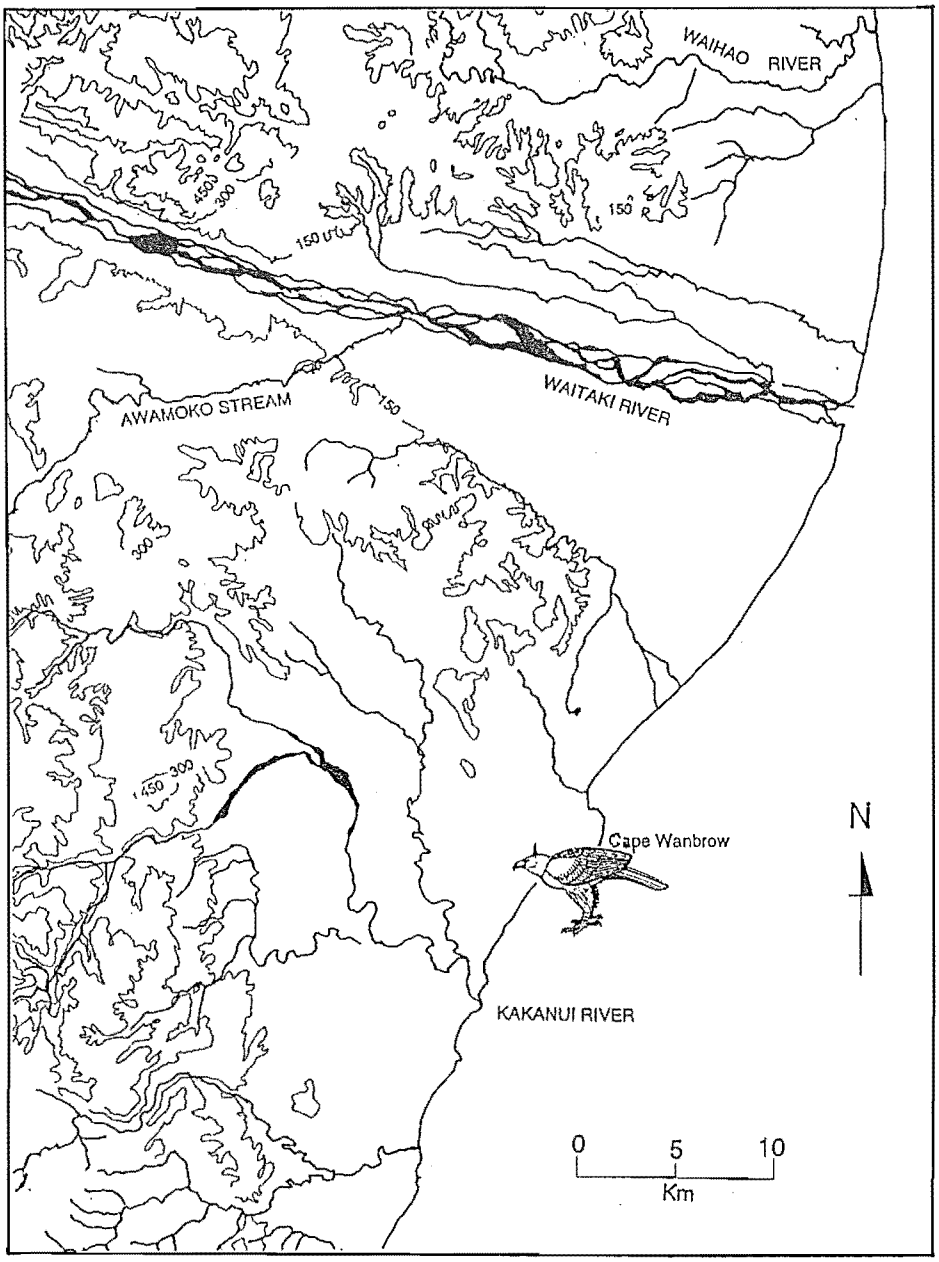

Fig. 8.20 Location of Oamaru/Cape Wanbrow sites, including Old Rifle Butts, and "Shirley Creek".

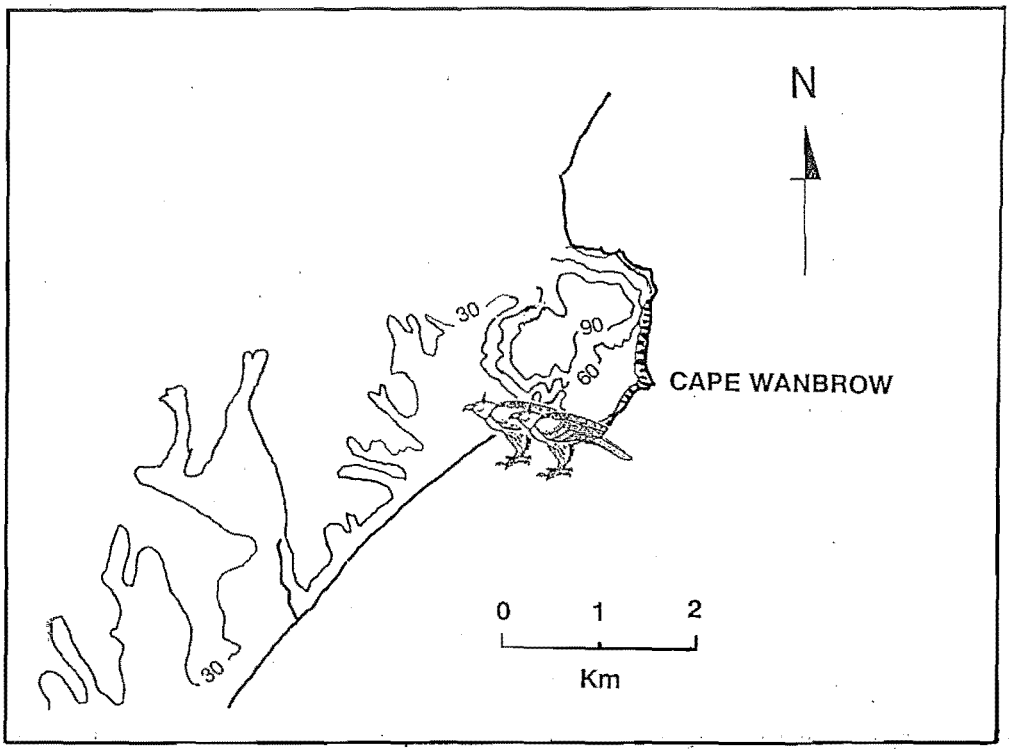

Fig. 8.21 (A-D) Old Rifle Butts site: A, general location, showing topography and drainage pattern in immediate area.

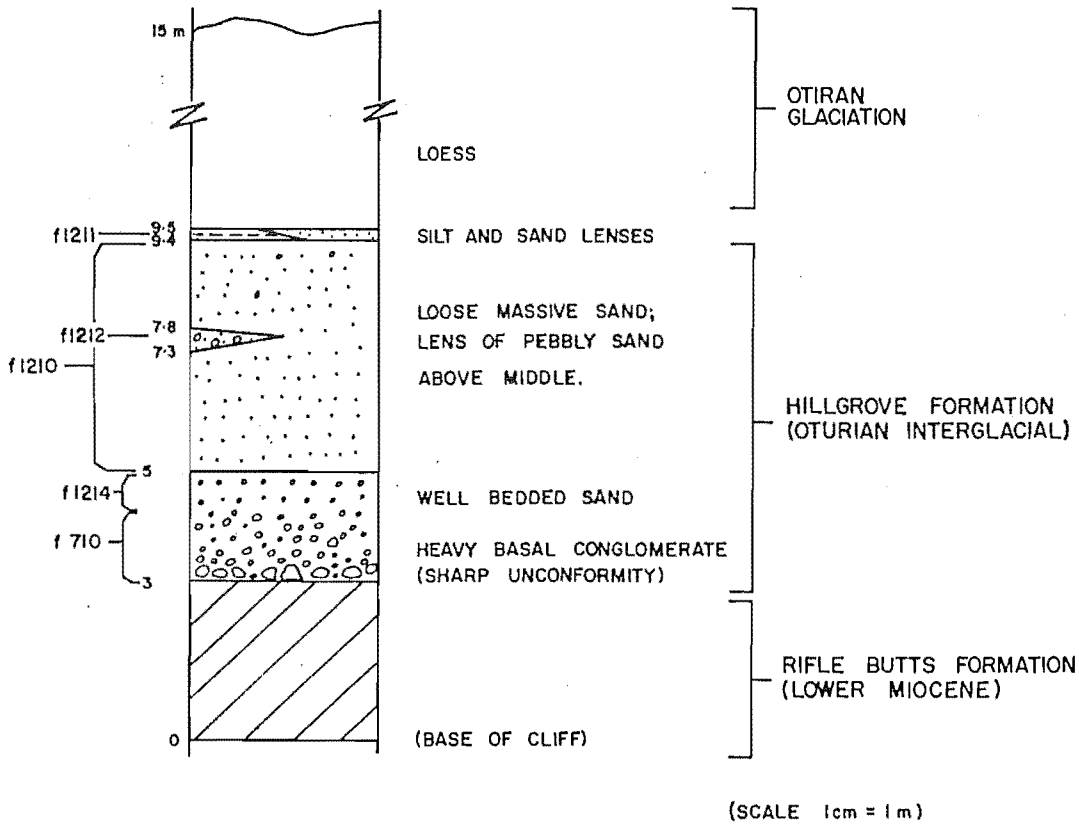

FIG. G2: CLIFF-SECTION AT NORTH END OF SOUTH OAMARU BEACH (OLD RIFLE BUTTS GRID REF. S136/542629)

Fig. 8.21B Section at Old Rifle Butts site, showing position of NZ fossil register site f1212, after Grant-Mackie & Scarlett (1973: 88).

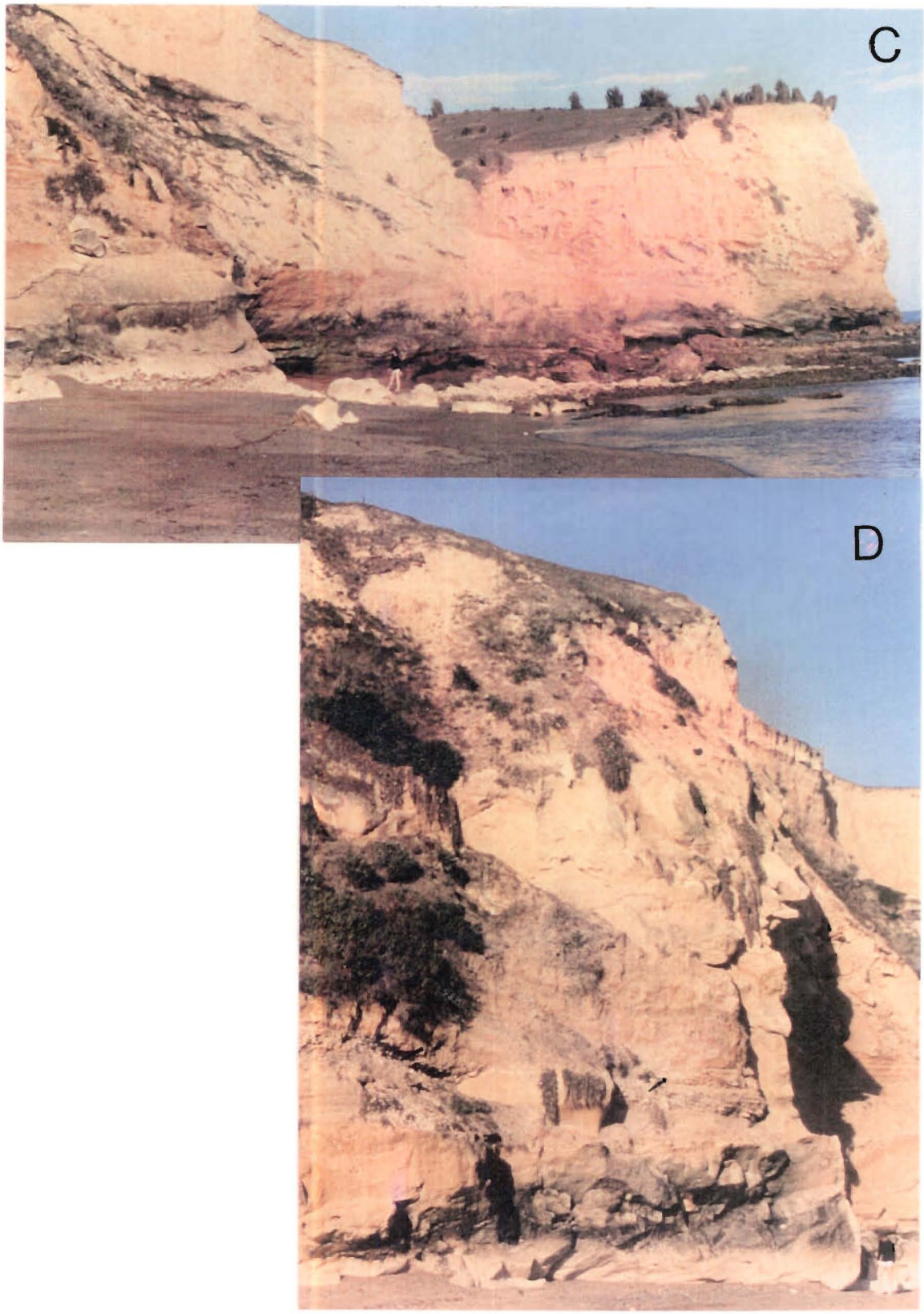

Fig. 8.21 (C, D) View east along southern side of Cape Wanbrow peninsula, showing entrance to Shirley Creek (around small headland 37 mm to right of figure in C), and fossiliferous layer (arrowed in D). Note thick capping of loess above fossil layer.

Otiran glacial times. The section as described by Grant-Mackie and Scarlett is:

5.5 m loess

0.1 m silt and sand lenses

2 m Basal conglomerate grading upwards into sandy conglomerate with marine molluscs and vertebrates, pebbles up to 150 mm

c3 m Miocene Old Rifle Butts Formation and Gee Greensand

A date of >35 900 ± 1700 years BP (no number) is given by Grant-Mackie & Scarlett (1973) for material from S136/f1212 from this locality. Three other dates are available for deposits of apparently similar age nearby (Table 3.2). All these dates are almost certainly minima, because of the very low collagen content in at least two (NZ3092 and 3093; W H Melhuish pers comm to T H Worthy 27 Feb 1989) and because the oldest date at least, approaches the limits of ^{14}C resolution.

The horizon in which the eagle bones were found (S136/f1212) has been lost through slumping, and the bone-bearing deposit has gone (Grant-Mackie & Scarlett 1973).

Material Pedal phalanx, ?, CM, AV 24887pt1; pedal phalanx, ?, CM, AV 24887pt; pedal phalanx, ?, CM, AV 24887pt; pedal phalanx, ?, CM, AV 24887pt; pedal phalanx, ?, CM, AV 24887pt; quadratojugal, L, CM, AV 24887pt; rib, ?, CM, AV 24887pt; vertebra - dorsal, CM, AV 24887pt; femur, L, CM, AV 24887pt; furcula, CM, AV 24887pt; radius, L, CM, AV 24887pt; radius, R, CM, AV 24887pt; scapula, R, CM, AV 24887pt; sternum, CM, AV 24887pt.

8.2.2.22 Oaro (Fig. 8.22 A,B)

NZMS260 O32/515551 42°30′00″S 173°30′00″E.

Nothing is known of this site, apart from its general locality, and the entry in the Canterbury Museum accession index noting that the material was deposited by O B Stanford in 1945. As this was the time at which the South Island Main Trunk railway was being built along that section of coast, it may be that the eagle material was recovered from a midden site or natural beach deposit disturbed during the construction. It is known that many Polynesian occupation sites were discovered, and artefacts removed, by construction crews along the course of the line in the late 1930s and 1940s.

Material Humerus, L, R, CM, AV 5333pt; radius, R, CM, AV 5333pt; scapula, L, CM, AV 5333pt; tibiotarsus, L, CM, AV 5333pt.

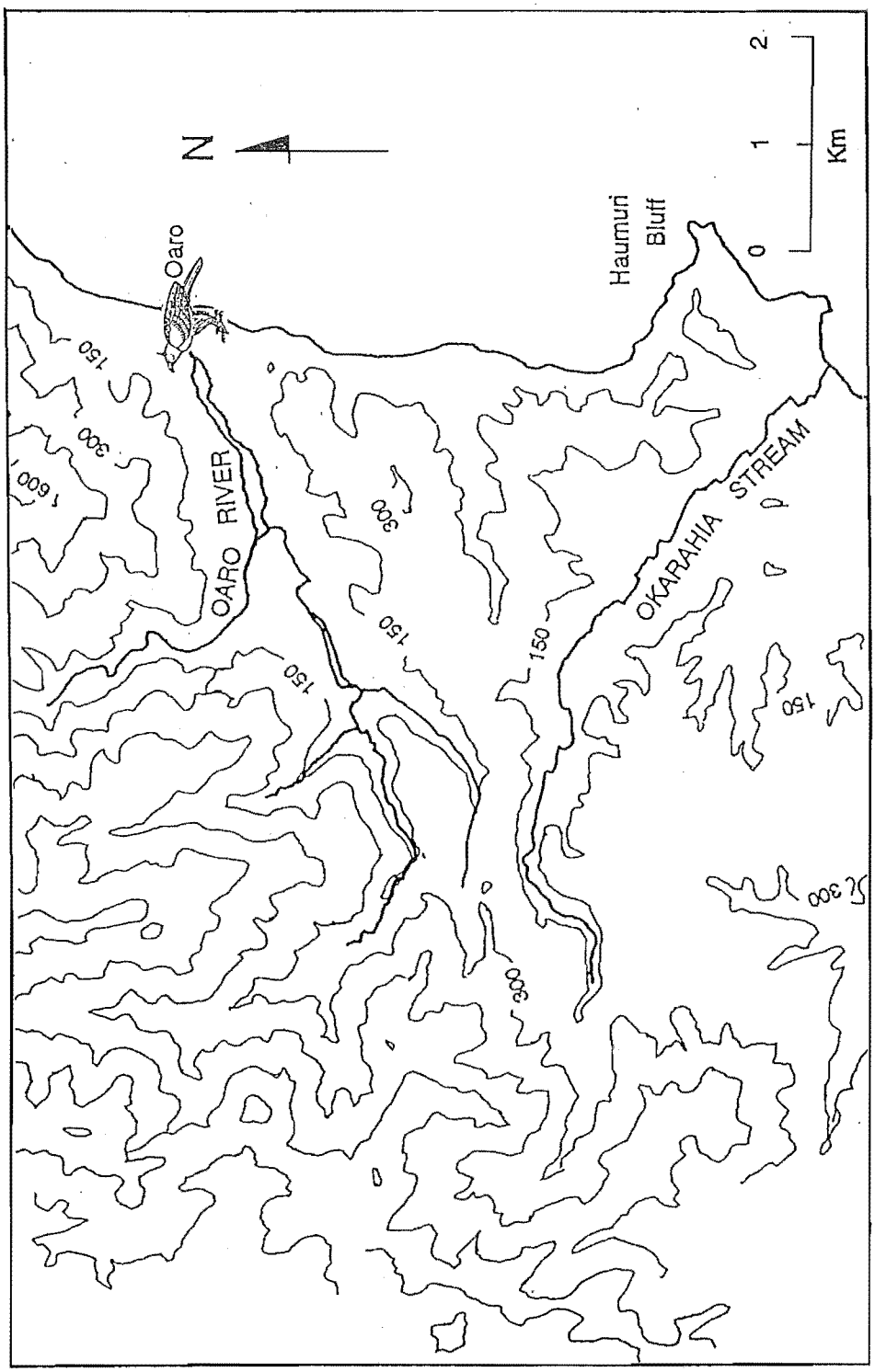

Fig. 8.22 (A, B) General area Oaro site (exact location of site unknown): A, showing topography and drainage pattern in immediate area.

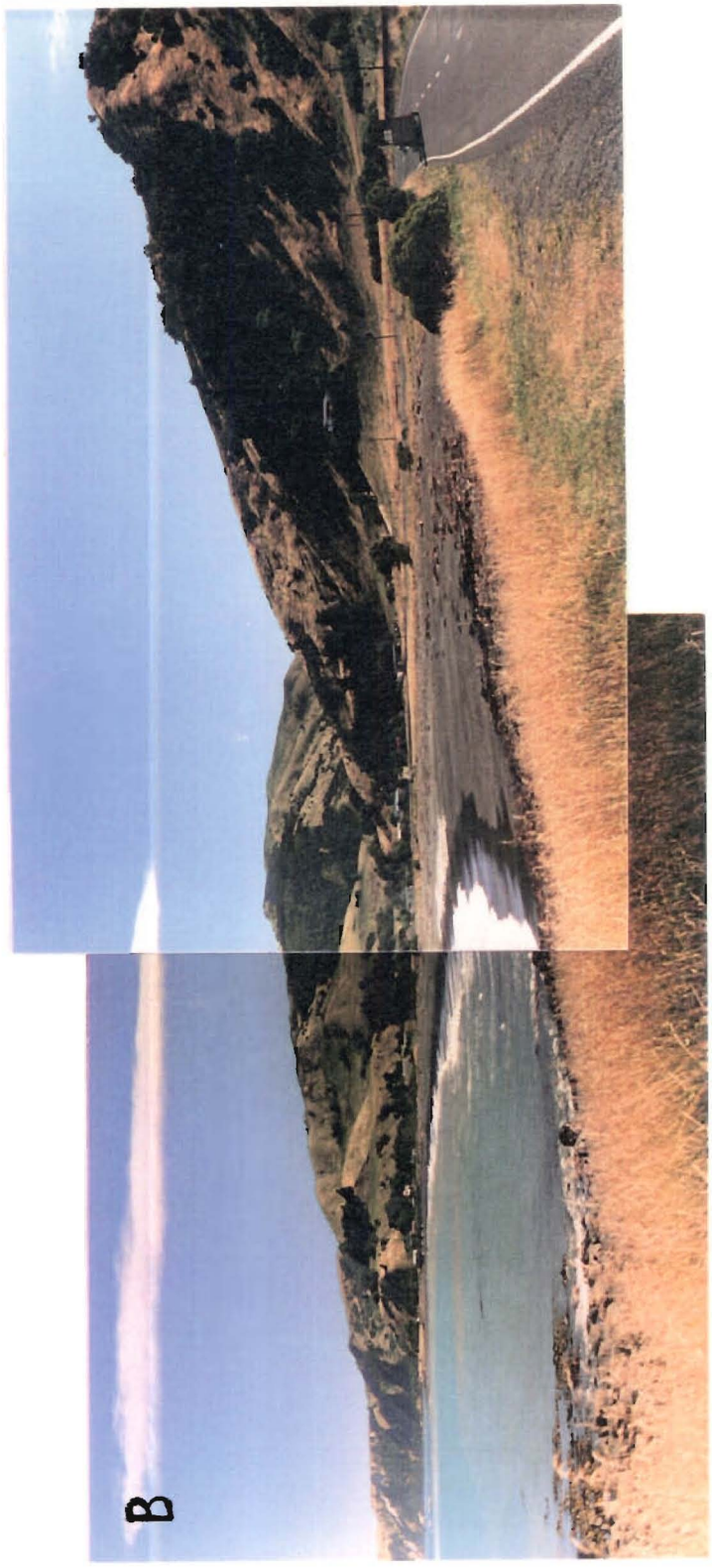

Fig. 8.22B View south along shoreline at Oaro, showing terrain of moderately steep coastal hills and mouth of Oaro River valley.

8.2.2.23 Obelisk Range (Fig. 8.23)

NZMS260 F42/095394 45°17′00″S 169°10′00″E.

This site was discovered in 1871 by W A Low. It was under an overhang (Hector 1874: footnote in Haast 1874), presumably on one of the schist tors characteristic of this range. The material was in the surface soil, and included moa, but these are not listed in the brief account by Hector (1872: footnote p. 114). The locality Cowes mentioned by Hector (1874) does not appear in current gazetteers, and was possible an ephemeral mining settlement on the Obelisk Range.

The eagle pelvis is still in excellent condition, and was described by Hector (1874: 63), as "in wonderful preservation, and is still covered with periosteum and has the capsular and some other ligaments adherant, while the osseous substance has lost hardly any of the original animal matter that it contained". Haast (1874: 71) described it as "belonging to a full-grown but still young individual". This, along with the type of site, suggests that it may represent a fully grown, but still dependant, young bird which died at the eyrie.

The age of the site is unknown.

Material 'Cowes', Obelisk Range, pelvis, BMNH, 75.12.15.34.

8.2.2.24 Orepuki (Fig. 8.24)

NZMS260 D46/038212 46°17′57″S 167°43′30″E.

Several specimens were collected from this site in 1945 and 1946. The area is similar to that at Wakapatu nearby to the east, where coastal dunes have both Polynesian and natural deposits. The material was presumably surface-collected during fossicking for Polynesian artefacts. The presence of a furcula is unusual in dune deposits, where the more robust pedal phalanges and limb bones are more common.

The material is probably of late Holocene age, if the dunes were formed after the Holocene high sea stand.

Material R M Forrest SMNZ pers comm. Pedal ungual phalanx, SMNZ, A 46.25; pedal ungual phalanx, SMNZ, A 46.26; pedal ungual phalanx, SMNZ, A 46.27; pedal ungual phalanx, SMNZ, A 46.28; pedal ungual phalanx, SMNZ, A 46.29; furcula, SMNZ, unnumbered.

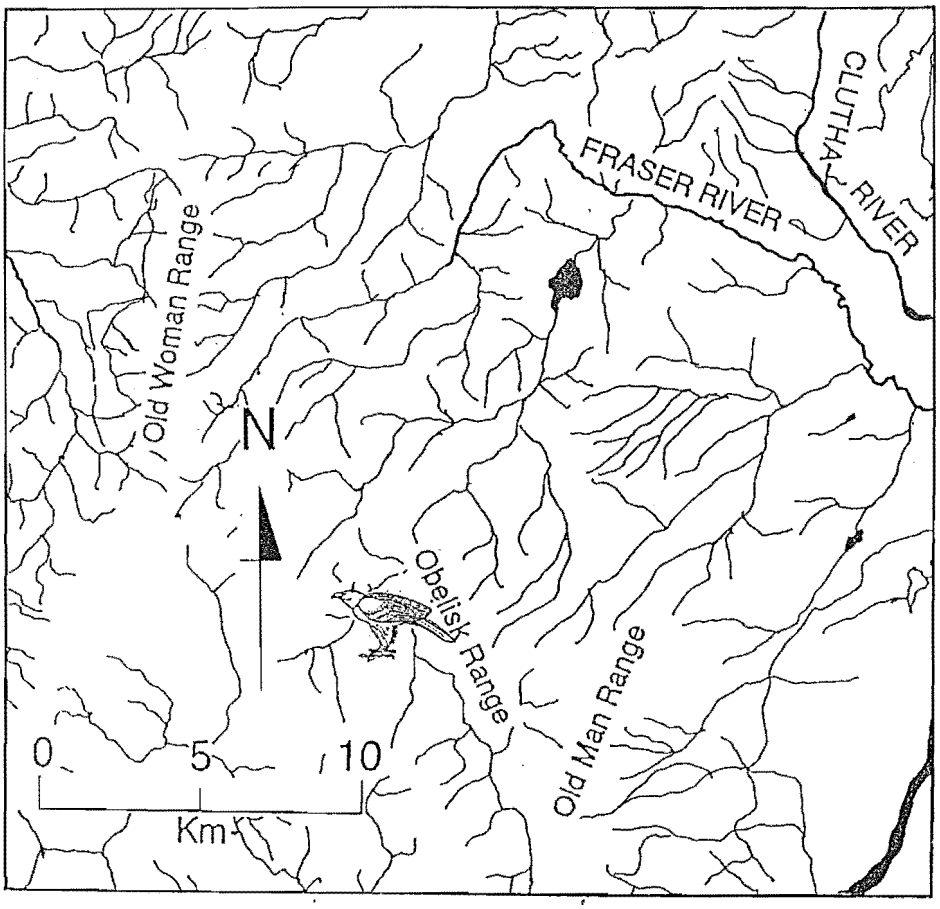

Fig. 8.23 Obelisk Range site area, central Otago, showing topography and drainage pattern. Exact position of site is unknown, but it was probably on one of the many rock outcrops near the edge of one of the stream gorges.

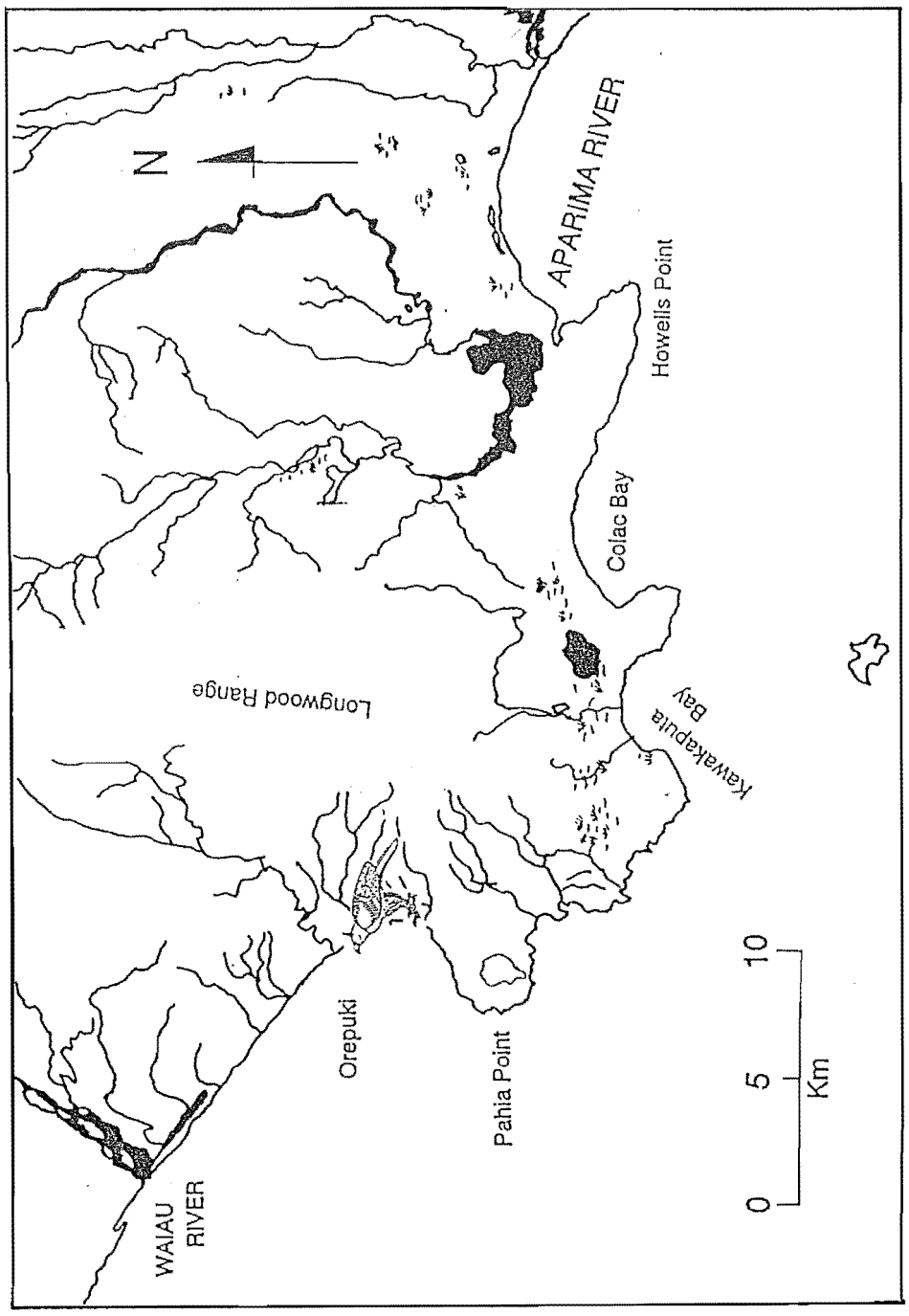

Fig. 8.15 Orepuki site, western Southland, showing topography and drainage pattern in immediate area. Site was probably in dunes along coast, and may have been associated with Polynesian occupation site.

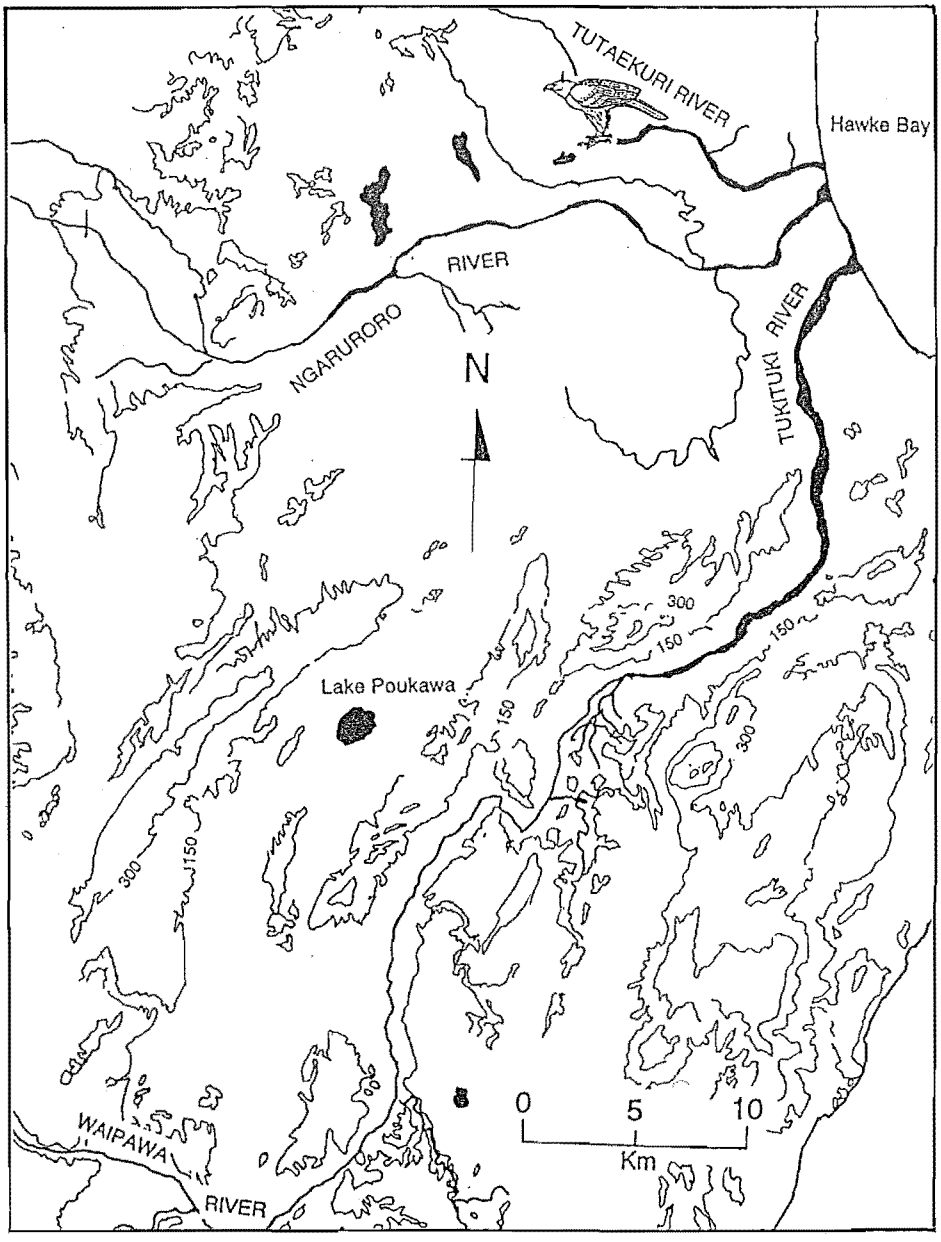

Fig. 8.16 Puketapu site area, southern Hawkes Bay, North Island, showing topography and drainage pattern. Exact position of site is unknown.

8.2.2.25 Puketapu (Fig. 8.25)

NZMS260 V21/363812 39°30′30″S 176°47′30′E.

This site was found when a swamp in a valley on the Greenmeadows estate at Puketapu near Napier was drained and the land ploughed (Hamilton 1889). Hamilton found "some" bones of *Harpagornis moorei* among "a few good bones of a small species of moa". These cannot now be identified in collections, but may be among the unprovenanced material labelled in Hamilton's hand in NMNZ. No notes or catalogue with an explanation of the numbers inked on these bones have yet been located.

Although this site may have been of Holocene age, two other sites in the area, Te Aute and Tangatupura, have been shown to be of probable Otiran age, and this possibility cannot be ruled out for Puketapu.

Material None identified in collections.

8.2.2.26 Pyramid Valley (Fig. 8.26 A-E)

NZMS260 M33/772038 42°59′30″S 172°35′50″E.

A deposit of fossil bones was discovered in this lake-remnant swamp (Fig. 8.26B) in 1936 by Messrs Hodgen, but the remains were stored in their woolshed for 2 years before the importance of the discovery was appreciated. In December 1938, it was brought to the attention of Dr R A Falla, director of the Canterbury Museum. From that time, various Canterbury Museum parties have excavated areas of the swamp. The first series began in early 1939, and extended into 1941, with 22 trips in 11 months of the two intervening years (Allan *et al.* 1941; map p. 331). Further excavations were carried out in 1942, 1948, and 1949, when a large area of the swamp was excavated (Duff 1949, 1955; Eyles 1955; Harris 1955; Hornibrook 1955; Scarlett 1955a, 1955b) (Fig. 8.26C). The swamp was re-opened in 1952 (to collect samples for ^{14}C-dating), 1965 and 1973, but has been permanently flooded and sealed by a lake since then (Burrows 1989).

The site is a stratified lake deposit, in a depression amongst hills of Weka Pass limestone. The swamp occupied an area of about 1.5 ha, and drained to the northeast (Falla 1941). In European times, the swamp was a shallow lagoon until drained (Anderson 1990), and then held a temporary lake when rainfall was

above average.

Bird bones have been found mainly in a layer of calcareous *gyttja* superimposed on a layer of blue clay. The latter lies above a thick layer of peat. The *gyttja* is covered by another peat layer (Percival 1941; Eyles 1955). Near the edge of the swamp, branches and tree trunks were present in the deposit, but apart from twigs of podocarp trees in the surface peat, parts of trees were not present further into the swamp. Beech (*Nothofagus*) leaves and other plant macrofossils were common in the lower layers of the *gyttja*.

The stratigraphy of a test pit in quadrat 70 of the 1949 excavations was, according to Eyles (1955) [metric conversions used here]:

[0.48 m] peat, mainly of *Carex secta*, with podocarp twigs

[1.07 m] yellow marl, or gyttja, discoloured with humus near the top; changing from the top downwards from light yellow with bands, with podocarp twigs and seeds, to darker banded yellow, to reddish brown near the base, where strongly laminated, then again from dark to light yellow over 0.36 m, with plant macrofossils (including *Nothofagus* leaves in the lowest light yellow zone. [The *gyttja* is a calcareous sediment derived from shells of freshwater ostracods - Crustacea, Ostracoda]

[0.43 m] blue-green 'pug' (silt); c 175 mm near the centre of the swamp; with

swamp tussocks protruding through from lower peat layer below; with many bivalves

[0.38 m] black peat, similar to surface peat; with decayed sedge tussocks extending through overlying sediments; with macrofossils of *Phormium*, *Typha* and moss.

[0.25 m] white limestone silt, with 2 species of bivalve mollusc.

[0.75+ m] blue-grey clay, similar to layer above, but with small pebbles of chert and limestone; of unknown depth.

Burrows (1989) figured a stratigraphic column that is basically the same as that described above but for the absence of the layer of silt above the lower peat. Burrows 1989) suggested that the basin held a sedge swamp until c 4280

BP, after which it contained a shallow lake for 1660-2500 years. Later the lake was infilled and choked with vegetation such as *Typha*, *Phormium*, and *Carex*. During the lake period, rapid biogenic sedimentation occurred, resulting in the laminated *gyttja*.

Most of the dates for moa bones from the swamp suggest that the birds involved were trapped about 3 500-3 600 BP. As noted by Burrows (1989), this fits with the dates from the top and bottom of the sequence (the oldest *gyttja* is younger than 4 280 BP, and the sediments formed in an uninterrupted sequence above the bones have been dated at 2930 BP). This suggests that the environment of deposition for most of the bones was a shallow lake with high carbonate concentrations.

Duff (1955) noted that few records were kept of the 1942 and 1948 excavations. Eyles (1955) described the excavation methods used in 1948, and in the major dig that lasted for 45 days from January 29 to April 4, 1949. The methods used in the early excavations were developed to ensure the full and rapid excavation of moa skeletons; quadrats were excavated in a drive along the swamp, with each being taken down to the basement and the spoil shovelled back on to the previous working floor (Eyles 1955). Although with this method "the chances of overlooking a moa bone were virtually nil, while even the fragile bones of forest birds were easily detected" (Eyles 1955: 259), the estimate of 75 minutes for the average recovery of a complete moa skeleton in the field (Eyles 1955) suggests that much smaller material was probably overlooked. Rich & Baird (1986) suggested that only rigorous sight collecting in association with wet-screening with small mesh screens can provide a sample that was not biased towards larger taxa.

Eagle bones were recovered in the first excavations, but most were collected during the 1949 field season. The preservation was excellent, and several of the smaller, more delicate elements are represented. Eyles (1955) discussed the problem of elements drifting from the mired carcases of moas in the liquid sediments. Some of the eagle elements that appear to come from a single individual (Table 8.7), were found many metres apart, and it seems likely that the more buoyant elements, such as the sternum, floated free in the water

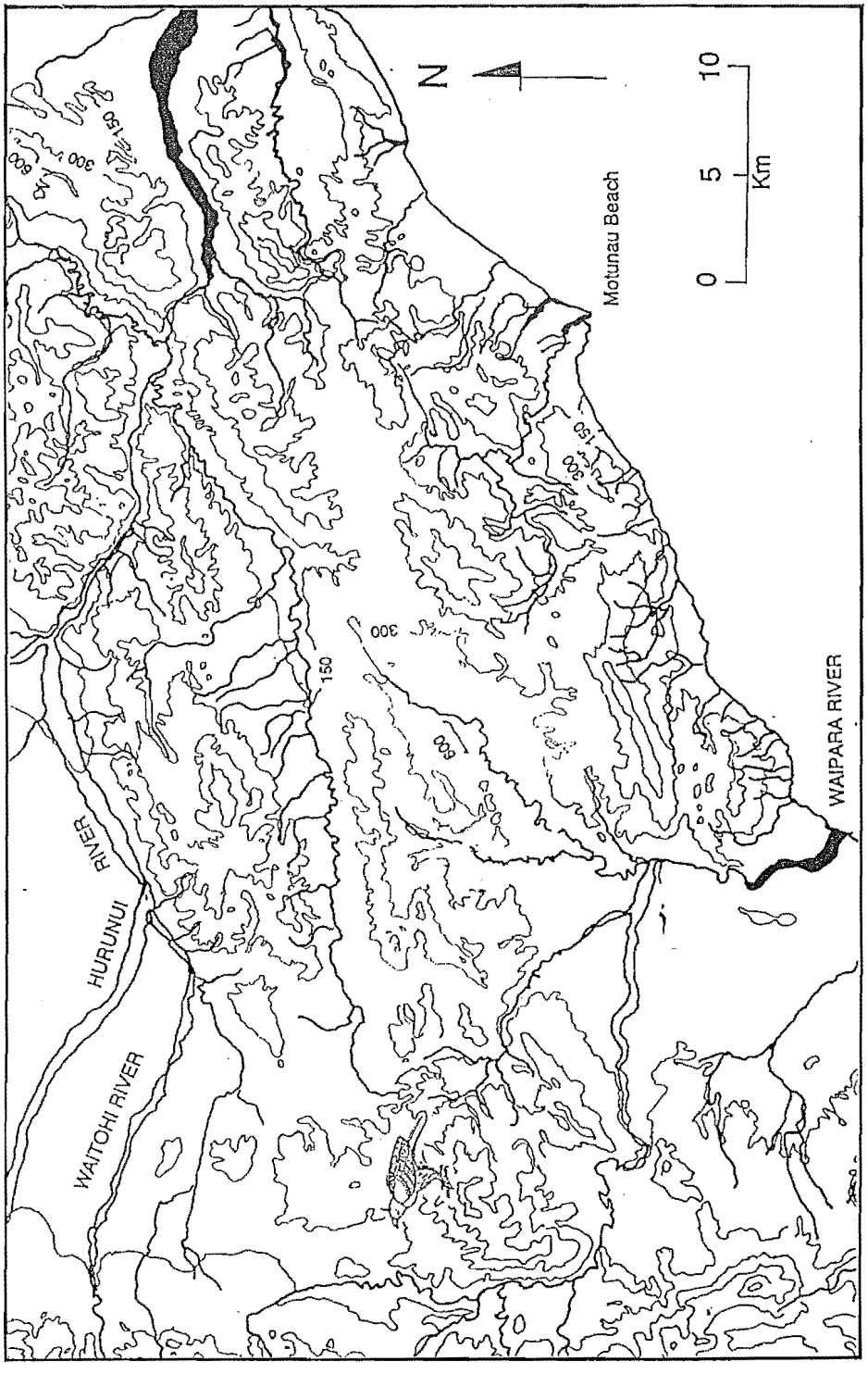

Fig. 8.26 (A-E) Pyramid Valley site, North Canterbury: **A**, showing topography and drainage pattern in immediate area.

Fig. 8.26B View north across Pyramid Valley swamp, now sealed by a lake to protect the remaining deposits (Photo: April 1988). Note low relief; richest part of deposit is near the top left (northwestern) end of the present lake.

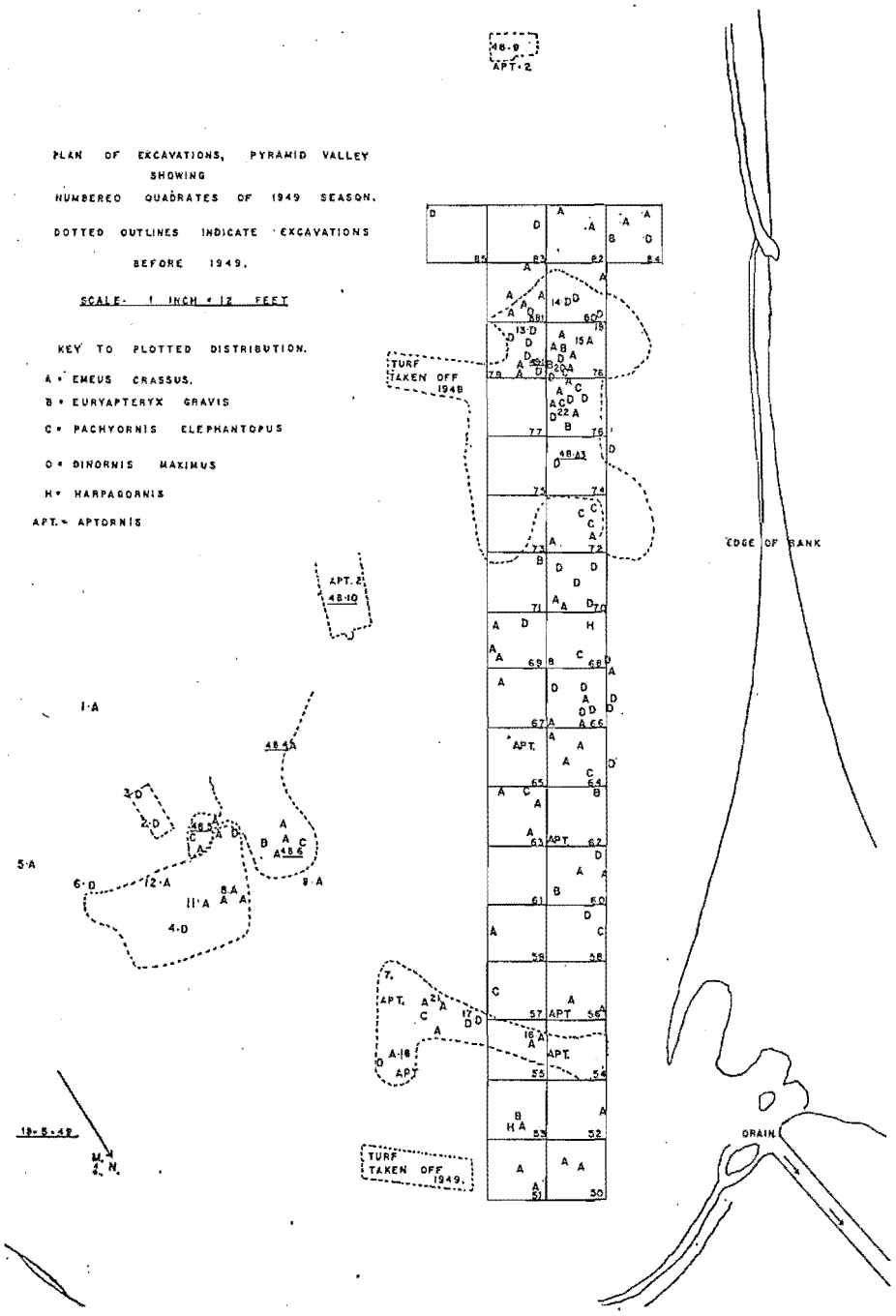

FIG. 1. Line diagram of excavations towards outlet of swamp, showing scattered excavations from 1939 to 1948 (dotted outlines) and planned quadrates of 1949. Distribution of moas shown by A (*Emeus*), B. (*Euryapteryx*), C. (*Pachyornis*), D. (*Dinornis*).

Fig. 8.26C Plan of early excavations, after Eyles (1955).

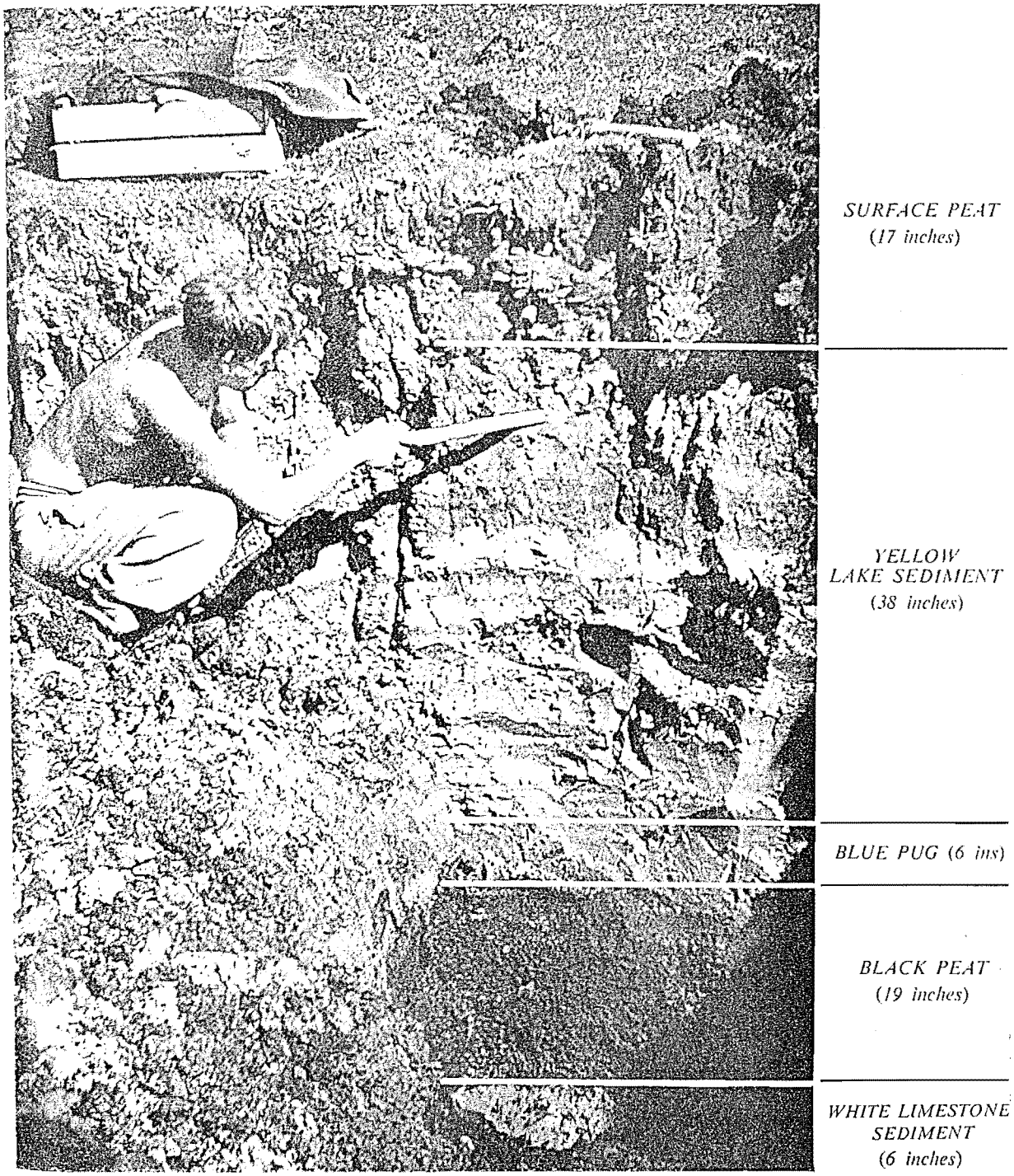

Fig. 8.26D Profile of swamp section, after Eyles (1955).

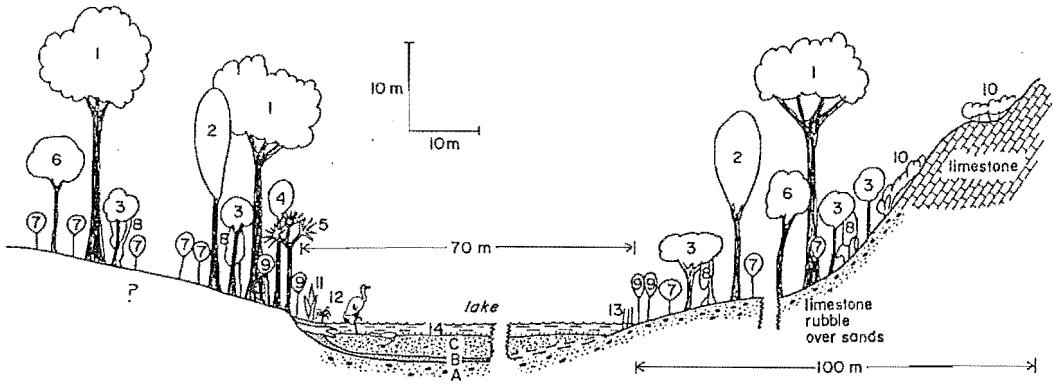

Figure 2: *Reconstruction of Pyramid Valley lake and surroundings, about 3500 years ago, facing north, based on macrofossil and pollen information from the lake sediments, and plant taxa from moa gizzards.*
Plant species: 1. *Podocarpus spicatus* 2. *Plagianthus regius* 3. *Pennantia corymbosa, Carpodetus serratus, Hoheria* sp. (probably *angustifolia*), *Myoporum laetum. Pseudopanax ferox* 4. *Elaeocarpus hookerianus* 5. *Cordyline australis* 6. Other small trees for which there are no definite records 7. *Melicope simplex, Myrtus obcordata, Coprosma rotundifolia, C.* spp. 8. *Muehlenbeckia australis, Rubus schmidelioides, R. squarrosus, Clematis* sp. (probably *foetida*), *Tetrapathaea tetrandra* 9. *Leptospermum scoparium, Phyllocladus alpinus, Myrsine divaricata, Olearia virgata, Coprosma* spp. 10. *Corokia cotoneaster, Teucridium parvifolium, Meuhlenbeckia australis, M. complexa, Rubus squarrosus, Carmichaelia* sp. 11. *Phormium tenax* 12. *Carex secta* 13. *Baumea* sp. (probably *rubiginosa*) 14. Characeae. A. Calcareous silt and clay, with limestone and chert pebbles. B. Sedge, *Phormium* and moss peat C. Calcareous ostracod gyttja.

Fig. 8.26E Reconstruction of vegetation in vicinity of lake at time of fossil deposition, after Burrows (1989).

column at some time during or after initial deposition. The accepted mode of entrapment for the large flightless birds at Pyramid Valley is that they walked or waded on to a crust of peat and vegetation extending out over the lake sediments and were mired as they broke through weak patches into the glutinous lake sediments below. This would not apply to smaller birds, such as songbirds, owls, and parrakeets; it is likely that many of these simply died and fell into the lake, where they sank, decayed, and their bones were incorporated into the softer lake sediments. Which of these scenarios applied to the eagles is not known. The scattering of bones, which matches the pattern of the smaller birds rather than the flightless species, suggests that some, at least, died in open water, perhaps having become waterlogged while attempting to catch prey bogged away from the shore. The excellent state of preservation of small, delicate bones suggests that they had not been transported far, and that they were deposited in a low-energy water environment because the abrasion and destruction of such material is rapid in higher energy environments (Napawongse 1981, quoted in Rich & Baird 1986). The most buoyant elements transported the furthest would have drifted with the gentle currents set up in the sheltered waters of the lake (Percival, in Allan *et al.* 1941).

The vegetation around the lake during the period of bone deposition has been described by Moar (1970), Gregg (1972), and Burrows (1989). A reconstruction in Burrows (1989: fig. 2, Fig. 8.26E) indicates a matai (*Prumnopitys taxifolia*) forest, with *Plagianthus regius*, *Pennantia corymbosa*, *Elaeocarpus hookerianus* and other forest trees and shrubs forming the main canopy and understorey, and a lake margin shrub belt, with open water on the lake. The plant taxa were identified from macrofossils, pollen (Moar 1970), and moa gizzard contents (Burrows *et al.* 1981). Burrows (1989) pointed out that, from the condition of many of the moa gizzards found associated with skeletons in the swamp, the carcases must have been covered by anaerobic sediments not long after death. That gut contents may outlast body tissue in a calcareous environment is shown by the presence of intact rumen contents associated with the skeleton of a cattle beast (*Bos taurus*) in a pothole at Annandale, North Canterbury, several years after its death (pers. obs.). Possibly the acidic contents

of the alimentary tract inhibit initial bacterial decay long enough for the material to be buried more or less intact. Rapid covering of the bones is also suggested by their usually good preservation.

Material Sq 68, vertebra, no process, CM, AV 5685pt; Sq 68, vertebra, with process 1, CM, AV 5685pt; Sq 68, vertebra, with process 2, CM, AV 5685pt; jugal bar, L, CM, AV 5685pt; quadrate, L, CM, AV 5685pt; quadratojugal, L, CM, AV 12356; sternum, CM, AV 6177pt; Sq 51, 53, prefrontal, ?, CM, AV 5684pt; Sq 51, 53, cranium, CM, AV 5684; Sq 51, 53, quadratojugal, L, CM, AV 5684pt; Sq 51, 53, quadratojugal, R, CM, AV 5684pt; Sq54, sternum, CM, AV 6012; Sq 60, femur, L, CM, AV 28366; Sq 68, cranium, CM, AV 5685pt; Sq 68, mandible, CM, AV 5685pt; Sq VII, mandible, CM, AV 12355; Sqs 84, 66, sternum, CM, AV 6177pt; humerus, L, CM, AV 5587.

8.2.2.27 Sumner (Fig. 8.27 A, B)

NZMS260 M36/898381 43°33′35″S 172°45′00″E.

The deposits in Moa Bone Point Cave were excavated by McKay for Haast in 1872 (Haast 1875). The list of material found in the cultural layers includes (p. 83) an "Awl made from distal end of tibia of *Ossifraga gigantea*, nelly [= *Macronectes giganteus* or *M. halli*, the giant petrels]". As noted by Falla (1942), Hutton corrected this to *Harpagornis* in the Canterbury Museum copy of the journal (now in Canterbury University library). The artefact was illustrated by Duff (1956) and is now in the Canterbury Museum ethnographic collection.

The only doubt as to the primary association of the eagle with man at this site is whether the bone was fresh when the artefact was fashioned from it. According to Falla (1942), the piece had every appearance of having been cut from fresh bone "having neither the colour nor bleaching associated with preservation in peat, clay, or dry sand". It is possible, but unlikely, that fossil 'industrial' bone was used to make this artefact, but this seems unlikely because of the abundance of suitable swan and albatross bones. Fossil eagle bone is, and probably always has been, rare on the surface in all areas, and in dunes or other sandy deposits such as those in the vicinity of the cave bone rapidly weathers and becomes brittle and unsuitable for working. The nearest known natural sites to Sumner are at least 60 km to the north, and the nearest surficial remains were probably those at Marfells Beach, further away still. Falla (1942) was probably correct in concluding that the artefact was worked from fresh bone, which implies that the bird was contemporary with humans at, or near, this site.

Material Tibiotarsus, R, CM, E.72.95.

8.2.2.28 Te Aute no. 2 (Fig. 8.28)

NZMS260 V22/220430 39°51′30″S 176°39′30″E.

Although Hamilton found no eagle bones at the first site excavated during the draining of the large Te Aute swamp, he excavated "several bones - amongst others an ungual phalanx ..., and several tibiae" of the eagle from the second, which was about 3.2 km up the main drain from its outfall through a ridge of limestone (Hamilton 1889). The first site was in a deep pool upstream of the cut through the limestone.

The eagle bones were found amongst moa bones at the foot of a spur extending into "an irregular winding lagoon forming the exit of the lake" through which the drain had been cut for 800 m. As the lake drained, the lagoon floor was exposed, and was found to "consist of a matted network of forest-roots and timber, together with innumerable seeds of hinau and manuka" (Hamilton 1889: 317). Hamilton suggested that "the action of the flowing water from the lake ... removed the accumulation of vegetable matter in which they were buried, and left the bones entangled among the roots and timber". He thought they were probably deposited at about the same time as those at Te Aute no. 1, where the sequence was (Hamilton 1889) [metric equivalents given]:

> [2.44-3.05 m] silt (pumice and material from surrounding Cretaceous rocks)
>
> [1.22± m] forest bed, consisting of trunks of trees and roots matted together; with moa bones
>
> The basement was stiff blue clay, with moa bones.

Because of the depth of the deposit, and its similarity to a dated site, Tangatupura, nearby, Worthy (1987) suggested that Te Aute was of Otiran age. This is supported by the size distribution of moa material from the site (Worthy 1987).

Material Pedal phalanges I/2, IV/5, ?, BMNH, R 3958-3960; tibiotarsus, R, NMNZ, DM 2144.

8.2.2.29 Waingongoro [=Ohawe] (Fig. 8.29)

NZMS260 Q21/125792 41°07′25″S 174°11′35″E.

Various early explorers fossicked at this site, now known as Ohawe, amongst

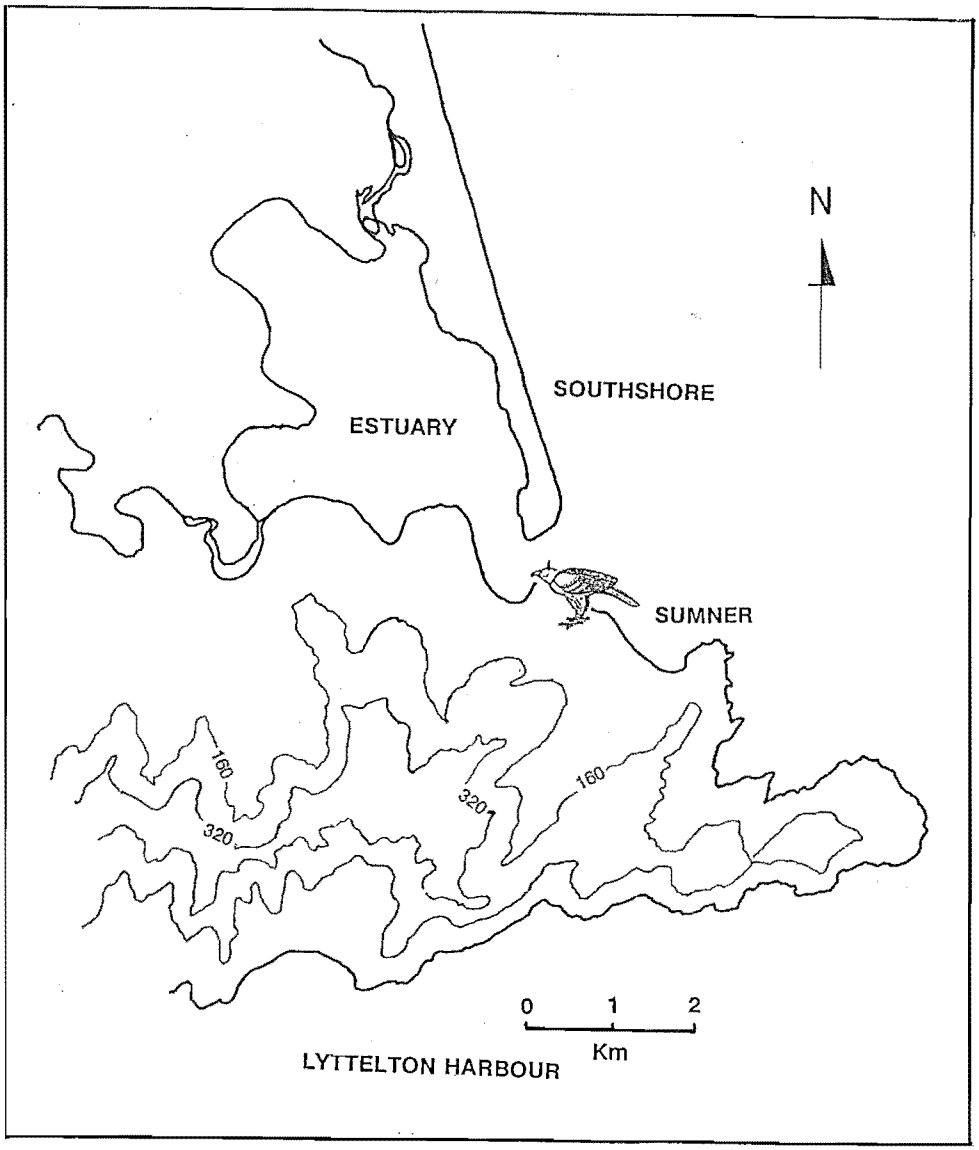

Fig. 8.27 (A, B) Sumner site: A, showing topography and drainage pattern in immediate area.

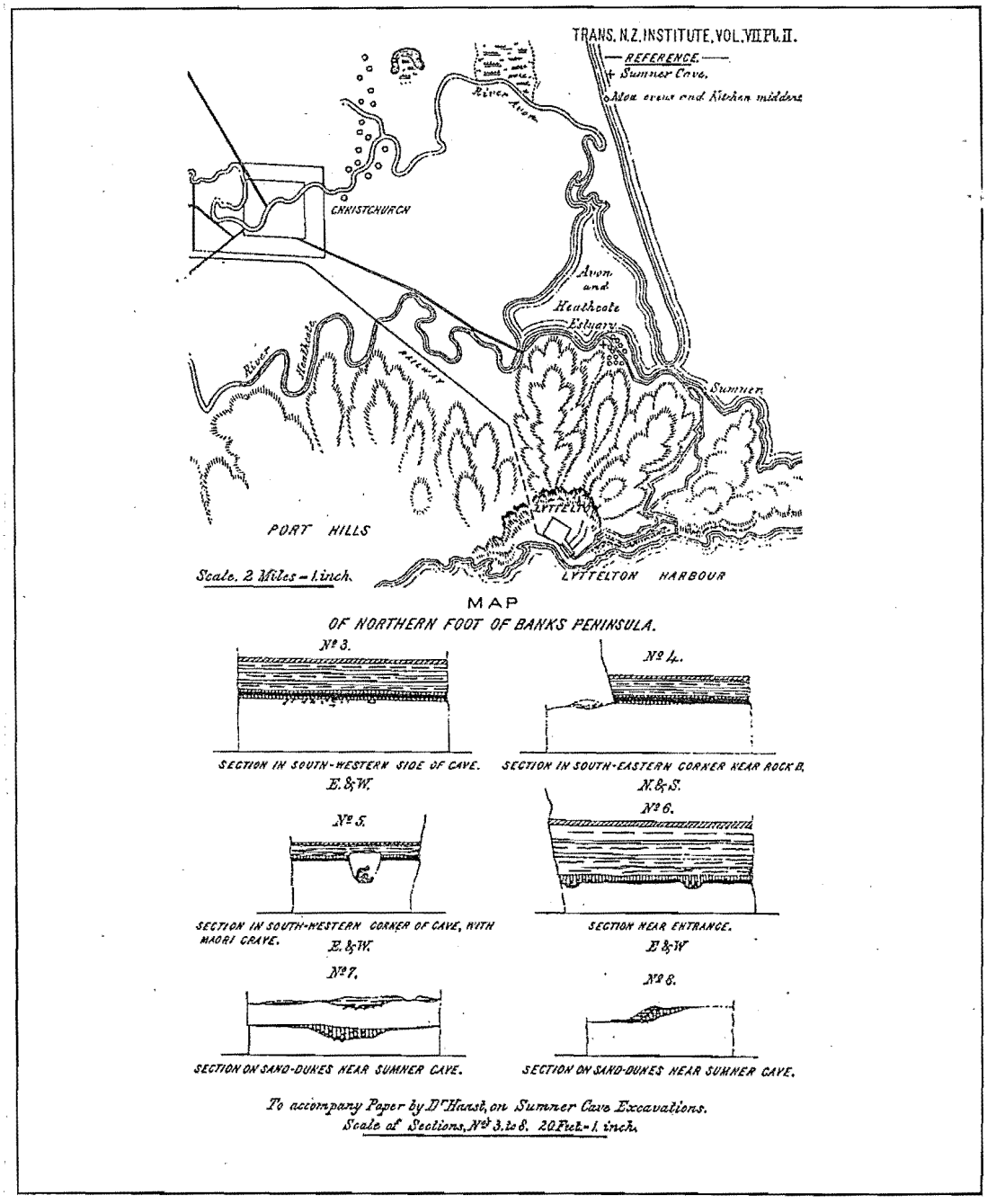

Fig. 8.27B Plan and profile of sections from excavations by McKay, after Haast (1875).

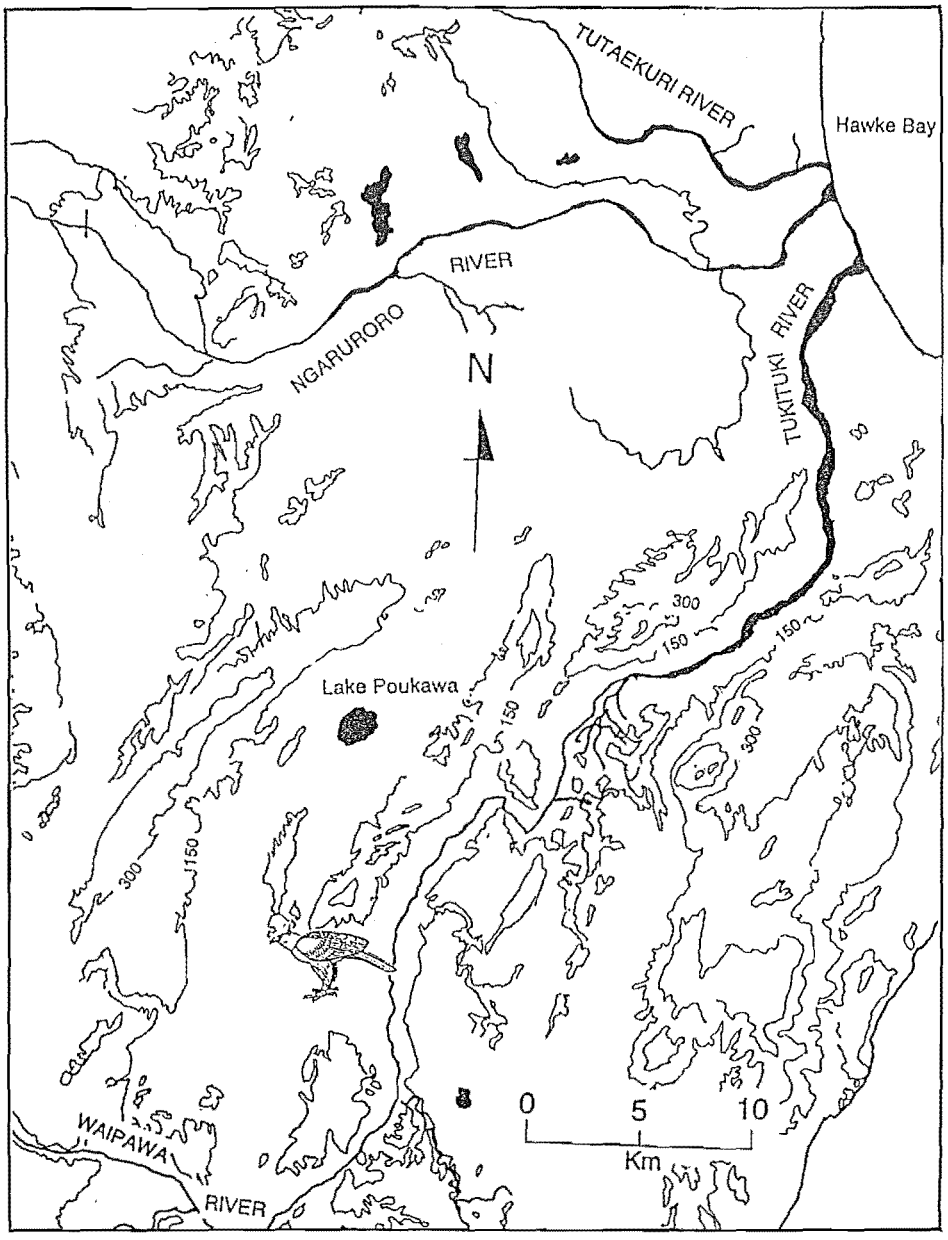

Fig. 8.28 General area of Te Aute site, Hawkes Bay, showing topography and drainage pattern. Exact position of site unknown, but it was near the outlet of the main drain cut in the late 1880s to drain the extensive Te Aute swamps. Note proximity of site area to Lake Poukawa, a major Holocene site (see text).

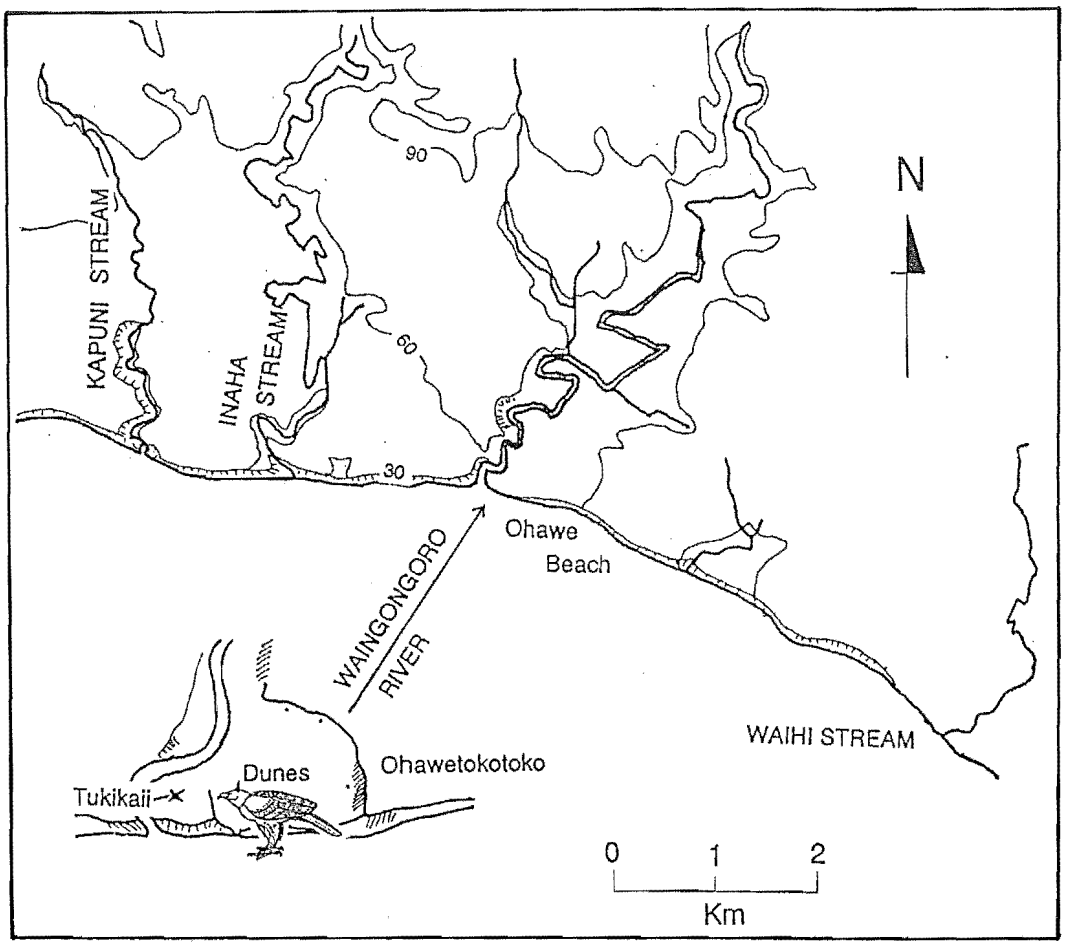

Fig. 8.29 Waingongoro site [= Ohawe, in archaeological literature], southern Taranaki, showing topography and drainage pattern in immediate area. Detail is from Mantell (1848).

them Richard Taylor and W B D Mantell. Mantell collected material, which included early and late Polynesian cultural horizons in the beach deposits. The single eagle bone in the collection was not recognised as such until Lydekker (1891) inspected and listed the collection over 30 years later (Millener 1981). There is therefore no evidence for a possible association of the bone with the cultural remains. Worthy has suggested to me that the origin of the eagle bone is uncertain, as Mantell seems to have mixed other material from his collections made at Waingongoro, which is in southern Taranaki, and Waikouaiti in the South Island. The bleached and leached appearance of the bone (Plate 16) is typical of dune material, and it is therefore almost certain that it came from Waingongoro rather than the peat swamp deposit at Waikouaiti.

Dates from cultural layers in the dunes range from 552±45 (NZ 717) to 1 018±49 (NZ 543) years BP. The dunes themselves are probably less than 6500 years old: Bussell (1988) reported that dune sands laid down 40 km east of Waingongoro, at Waverley, were deposited 6 600-≥5750 years BP and again at <5700 years BP. According to Gibb (1983), the sea reached its present level about 6 500 years BP.

Material Manus II/1, L, BMNH, 32245h.

8.2.2.30 Waipapa Point ("Waipapapa") (Fig. 8.30)

NZMS260 F47/920861 46°39′40″S 168°50′50″E.

An ungual phalanx in NMNZ labelled "Waipapapa" probably comes from a site on what is now known as Waipapa Point, east of Invercargill, in Southland. The southern Maori dialect contained an extra terminal 'pa' (P M Johns pers. comm.) and G M Thomson refers to a Waipapapa Point between Catlins River and Dog Island in a paper on the coastal fish of Otago (Thomson 1892). The handwriting on the bone seems to be Hamilton's, and the bone probably came into his possession when he was Registrar at Otago University, in the late 1890s and early 1900s. It was not mentioned in his principal paper on the eagle (Hamilton 1893), so was probably collected after that year.

Material Pedal ungual phalanx, NMNZ, DM 7074, A Hamilton?

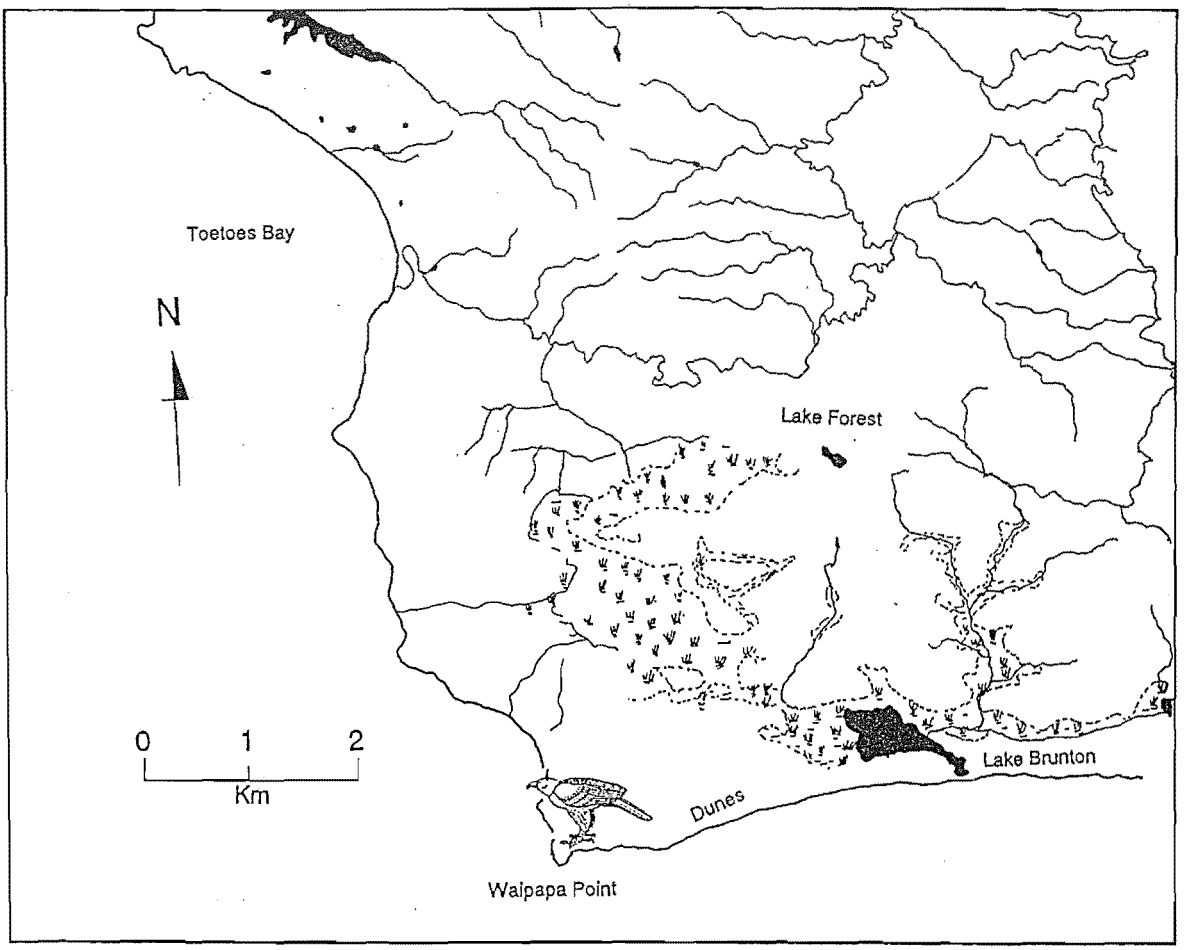

Fig. 8.30 General location of Waipapa Point site [Waipapapa of Hamilton], eastern Southland, showing topography. Exact position of site unknown, but it was probably in the dunes near the Point.

8.2.2.31 Wairau Bar (Fig. 8.31)

NZMS260 P28/986660 41°30′30″S 174°03′45″E.

Falla (1942) recorded a single ungual phalanx from excavations at this important moa-hunter site, which was discovered by J R Eyles in 1942 and excavated by Eyles, R Duff, O Wilkes, and others, at various times from then into the 1960s. The deposit is in beach gravels and sand at the end of the boulder bank that separates the Vernon Lagoon from the sea, at the mouth of the Wairau River. The bank developed after present sea level was established about 6 500 years BP (Gibb 1983, Pickrill 1976), because the former coastline (now marked by a line of dunes) was then several kilometres inland (Brown 1981).

Three artefacts fashioned from eagle bone were found in later excavations; the comments on the Sumner Cave artefact (p. 208) also apply here. Although the eagle may been deposited naturally at the site within the past 3 000-4 000 years, the artefacts are almost certainly evidence that they occurred nearby within the past millenium and were known to Polynesians.

Dates from the cultural layers range between 587±58 (NZ1838) and 909±48 (NZ50) years BP. The maximum age for material at the site would be 6 500 years, when the sea reached its present level (Gibb 1983).

Material Pedal ungual phalanx, CM, AV 12354; tibiotarsus, L, CM, 771; ulna, L, CM, 1780; ulna, R, CM, 1781; pedal ungual phalanx, CM, AV 36337, S29/2?.

8.2.2.32 Wakapatu (Fig. 8.32 A, B)

NZMS260 D46/140142 46°22′10″S 167°51′10″.

This site was excavated in 1932 by D Teviotdale, who was primarily interested in early Polynesian occupation and artefacts. Eagle bones labelled Wakapatu, Teviotdale 1932, were probably collected during his excavation of the site, but there is no indication that the material was associated with the human occupation levels. It is one of a series of five similar sites between Warrington, north of Dunedin, and Orepuki, just west of Wakapatu itself. The site is at the southern end of the forested Longwood Range, on a sand barrier beach near Lake George.

No dates are available for this site, but a lower limit on the age of the

material is provided by the cultural layers, and an upper limit by the probable maximum age of the dunes at about the mid Holocene.

Material Pedal phalanx I/1, L, OMNZ, ?; pedal phalanx I/1, R, OMNZ, ?; pedal phalanx II/1, ?, OMNZ, ?; pedal phalanx II/2, R, OMNZ, ?; pedal phalanx III/2, ?, OMNZ, ?; pedal phalanx III/3, ?, OMNZ, ?; ? tibiotarsus, OM C 32.66pt, catalogue only, not seen; [or Ngapara] tarsometatarsus, OMNZ C 32.67pt, not seen, catalogue only; tibiotarsus, OMNZ, C 32.66pt, not seen, catalogue only; [or Ngapara] tarsometatarsus, OMNZ, C 32.67pt, not seen, catalogue only.

8.2.2.33 Warrington (Fig. 8.33)

NZMS260 I44/226965 45°43′00″S 170°35′40″E.

This site was in dunes and may have been associated with extensive early Polynesian deposits. Hamilton (1893) noted that it was "from the Maori middens at Warrington", but earlier (Hamilton, *Lyttelton Times* 26 May 1892) wrote: "I was at Warrington on Tuesday, and picked up a very perfect metatarson of the smaller form of harpagornis on the sandhills" (Hamilton 1892).

On dune formation, this bone cannot be older than c 6 000 years; if it were associated with the cultural horizons, it would not be older than 1 000 years.

Material Tarsometatarsus, L, NMNZ, DM 2137, A Hamilton, May 1892.

8.2.2.34 UNPROVENANCED MATERIAL "Nelson", pelvis, CM, AV 5332, CAST; pedal phalanx, ?, NMNZ, DM 2143pt1; pedal phalanx, ?, NMNZ, DM 2143pt2; pedal phalanx, ?, NMNZ, DM 2143pt3; pedal phalanx, ?, NMNZ, DM 2146pt; quadrate, L, CM, AV 9845; rib fragment, ?, NMNZ, DM 2146pt; rib fragment, ?, NMNZ, DM 2146pt; coracoid, R, CM, AV 5339; coracoid, R, NMNZ, DM 2146pt; cranium, NMNZ, DM 2146pt; femur, L, NMNZ, DM 2138; femur, R, NMNZ, DM 2145pt; furcula, L, NMNZ, DM 2146pt; humerus, R, NMNZ, DM 2146pt; pedal ungual phalanx, CM, AV 10472; sternum, CM, AV 15965; tarsometatarsus, R, NMNZ, DM 2139; tibiotarsus, L, NMNZ, DM 2146pt; tibiotarsus, R, NMNZ, DM 2145pt.

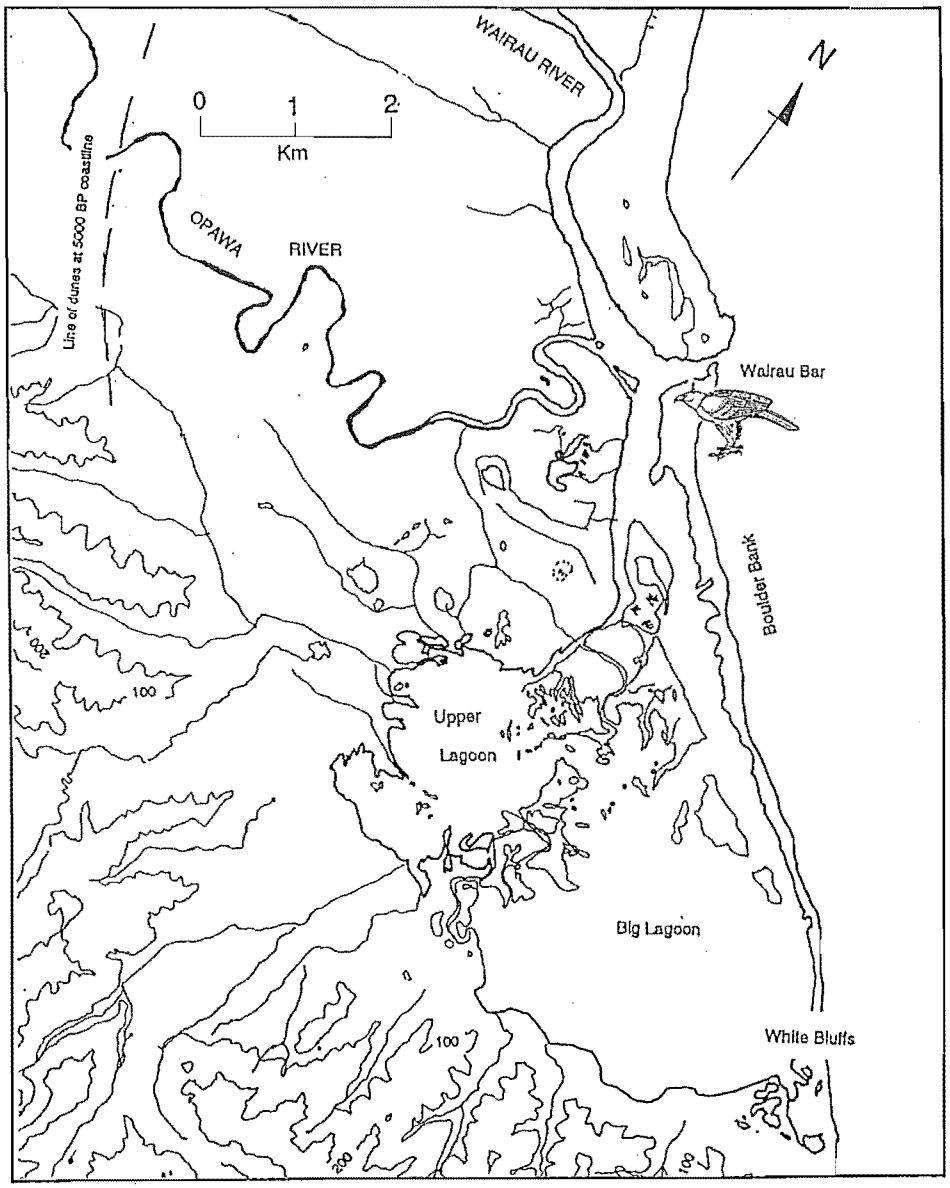

Fig. 8.31 Wairau Bar site, showing location and low relief of the surrounding area. The early Polynesian occupation sites are clustered near the northern (river mouth) end of the Boulder Bank. towards the landward side of the spit.

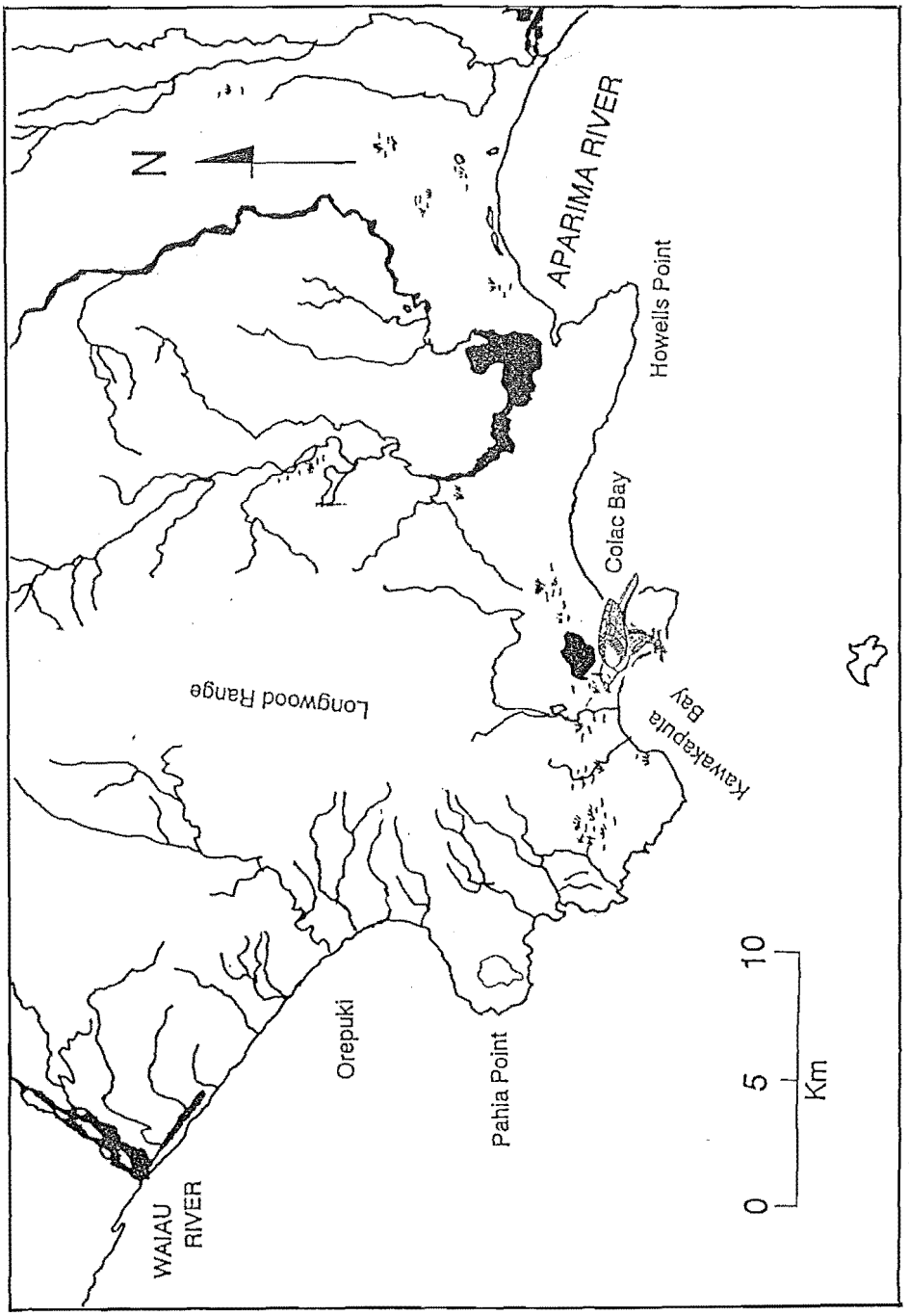

Fig. 8.32 (A, B) General location of Wakapatu site, western Southland: A, showing topography and drainage pattern; exact position of site is unknown, but it was probably in the dunes, near the base of the spit.

Fig. 8.32B View from eastern end of sand spit at Wakapatu, north over Lake George to Longwood Range (altitude 800 m); Wakapatu site probably in dunes in foreground. Photography: December 1988.

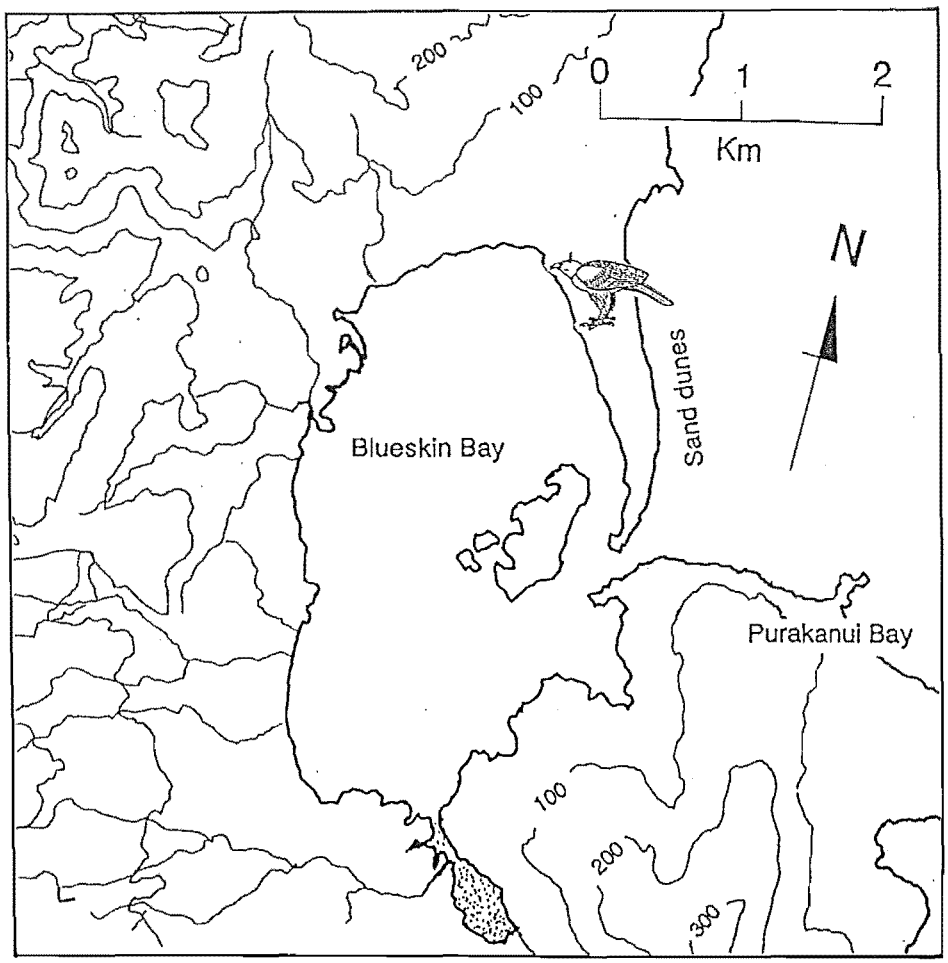

Fig. 8.33 General location of Warrington site, north of Dunedin, showing topography and drainage pattern. Site was in dunes of the bay bar.

8.3 DISTRIBUTION

8.3.1 General

The 41 sites at which eagle material has been found are listed in Table 8.1. Map co-ordinates are given as precisely as possible, but accuracy varies from the nearest metre for cave grids, to the closest 10 000 metre (or yard) square on the appropriate topographical map for sites given as general localities. A reference to 'Nelson' on a cast of a pelvis (CM AV 5332) is not listed. There is no mention in the literature of any material from Nelson from which this cast could have been taken. It is likely to be a cast of the pelvis found in the Obelisk Range and now at BMNH.

The distribution of localities relative to the present coastline is shown in Fig. 8.34 and Fig. 8.35 (A-G). Of the 37 South Island sites, only one cannot be used to delimit the bird's former range. The Moa Bone Cave, Sumner, record is based on a single artefact [awl, CM/E.72 95, from the distal end of a tibia (Duff 1956)], and could have been carried some distance to the site. Other South Island records (Cannibal Bay, Wairau Bar, Marfells Beach, Orepuki, Waipapa Point, Wakapatu, and Warrington) could also be from cultural deposits (especially awls CM 771, 1780, 1781 from Wairau Bar).

As noted by Millener (1981), the four accepted North Island sites were all discovered before 1900. Recent reports from Great Exhibition Bay and the Coromandel Peninsula were misidentifications (Millener 1981). Discovery dates for South Island sites range from 1871 at Glenmark to the present (Honeycomb Hill). The first North Island record was from Waingongoro before 1850, but the specimen was not identified until much later (Lydekker 1891).

8.3.1.1 *Altitude, topography, and palaeotopography* The approximate altitude of each site is given in Table 8.1. For those sites which could not be accurately located geographically, the altitude of the most likely location is given. As most sites are in areas of relatively low relief, this is not likely to have introduced any significant error (± 20 m). Sites in areas of stronger relief, such as those on the Obelisk and Dunstan ranges, are given as ≥1000 metres, because of the

Table 8.1 Sites where bones of *Harpagornis moorei* have been reported. T, type of site: S, swamp; C, cave; F, fissure; R, rockshelter; D, dunes; L, loess bed; B, beach; M, midden. A, approximate age of site; I, North (N) or South (S) Island; *, some or **, all material lost or not located, or more material reported than presently known. Alt/sea: altitude (metres); D, distance to nearest coast (kilometres). Details of level of accuracy for each location are given in the text. Continued on next page.

					Map ref.	Alt/sea		Co-ordinates	
Site name	T	A	I	*	NZMS 260	Alt m	D km	Lat (S)	Long (E)
Albury Park	S	H	S		J38 330662	310	41	44 11 30	170 47 50
AR 144	C	P	S		L27 421092	240	8	41 07 25	172 11 30
Cannibal Bay	D	H	S		H46 606108	<10	0	46 28 00	169 45 20
Castle Rocks	F	H	S		E44 435786	300	65	45 48 30	168 17 00
Dunstan Range	?	H	S		G39/40	>1000	115	44 35 00	169 45 00
E entrance	C	P	S		L27 421092	240	8	41 07 25	172 11 30
Eagle Roost	C	P	S		L27 421092	240	8	41 07 25	172 11 30
Enfield	S	H	S		J41 429723	60	11	45 02 01	170 52 20
Glenmark Creek	S	P	S		N33 920004	<100	13	43 01 00	172 47 00
Glenmark/East	S	H	S		N34 921993	85±	13	43 01 00	172 47 00
Glenmark/West	S	H	S	*	N34 921992	85±	13	43 01 00	172 47 00
Glenmark Creek 2	S	P	S	**	N33 920004	<100	13	43 01 00	172 47 00
Golden Point	S?	H?	S	**	I42 084365	350	32	45 21 05	170 25 40
Graveyard	C	P	S		L27 421092	240	8	41 07 25	172 11 30
Hamilton Swamp	S	H	S		H42 862468	630	55	45 15 10	170 09 30
Hamilton Gully	L?	?	S		H42 845469	500	55	45 15 10	170 08 10
His Cave	C	P	S		L27 421092	240	8	41 07 25	172 11 30
Hives extension	C	P	S		L27 421092	240	8	41 07 25	172 11 30
Holyoake Stream	C	P?	S	*	N26 017216	150±	4	41 01 00	172 56 00
Hunterville	?	P?	N	**	S22 296364	260	40	39 57 00	175 34 15
Kakanui Beach	S	H	S		J42 450560	<10	0	45 11 20	170 54 10
Kapua	S	H	S		J40 509011	100	14	44 46 55	170 59 20
Kings Cave	C	H	S		J38 402511	300	25	44 19 30	170 52 15

Table 8.1 continued Sites where bones of *Harpagornis moorei* have been reported. T, type of site: S, swamp; C, cave; F, fissure; R, rockshelter; D, dunes; L, loess bed; B, beach; M, midden. A, approximate age of site; I, North (N) or South (S) Island; *, some or **, all material lost or not located, or more material reported than presently known. Alt/sea: altitude (metres); D, distance to nearest coast (kilometres). Details of level of accuracy for each location are given in the text.

Site name	T	A	I	*	Map ref.	Alt m	D km	Lat (S)	Long (E)
Marfells Beach	D	H	S		P29 095421	<10	0	41 43 25	174 11 40
Motunau	S	P	S		N34 194005	60±	2	43 00 30	173 30 00
Mount Owen	C	H	S		M28 715615	1600	44	41 33 15	172 32 15
Ngapara	F	H	S		J41 785308	260	23	44 58 50	170 43 40
Oaro	?	H?	S		O32 515551	<100	0	42 30 00	173 30 00
Obelisk Range	R	H	S		F42 095394	>1000	115	45 17 00	169 10 00
Old Rifle Butts	B	P	S		J41 501627	<10	0	45 07 35	170 58 00
Orepuki	D	H	S		D46 038212	<20	0	46 17 57	167 43 30
Puketapu	S	H?	N	**	V21 363812	30	9	39 30 30	176 47 30
Pyramid Valley	S	H	S		M33 772038	335	25	42 59 30	172 35 50
Shirley Creek	B	P	S		J41 503627	<10	0	45 07 35	170 58 01
Sumner	M	H	S		M36 898381	<10	0	43 33 55	172 45 00
Te Aute no. 2	S	P	N	*	V22 220430	75	25	39 51 30	176 39 30
Waingongoro	D	H	N		Q21 125792	<10	0	39 35 20	174 11 35
Waipapa Point	D	H	S		F47 920861	<10	0	46 39 40	168 50 50
Wairau Bar	M	H	S		P28 986660	0-2	0	41 30 30	174 03 45
Wakapatu	M?	H	S		D46 140142	<10	0	46 22 10	167 51 10
Warrington	M?	H	S		I44 226965	<10	0	45 43 00	170 35 40
Total	41								

Cave co-ordinates from Honeycomb Hill cave maps (metre grid); for Mount Owen, this indicates New Zealand Speleological Society code for pothole on the Mt Owen massif.

Site in Honeycomb Hill/Mt Owen	Northing	Easting
AR 144	820	780
E entrance	1780	1070
Eagle Roost	1340	965
Graveyard	1350	1040
His Cave	534	110
Hives extension	1295	962
Mount Owen	SO 209	

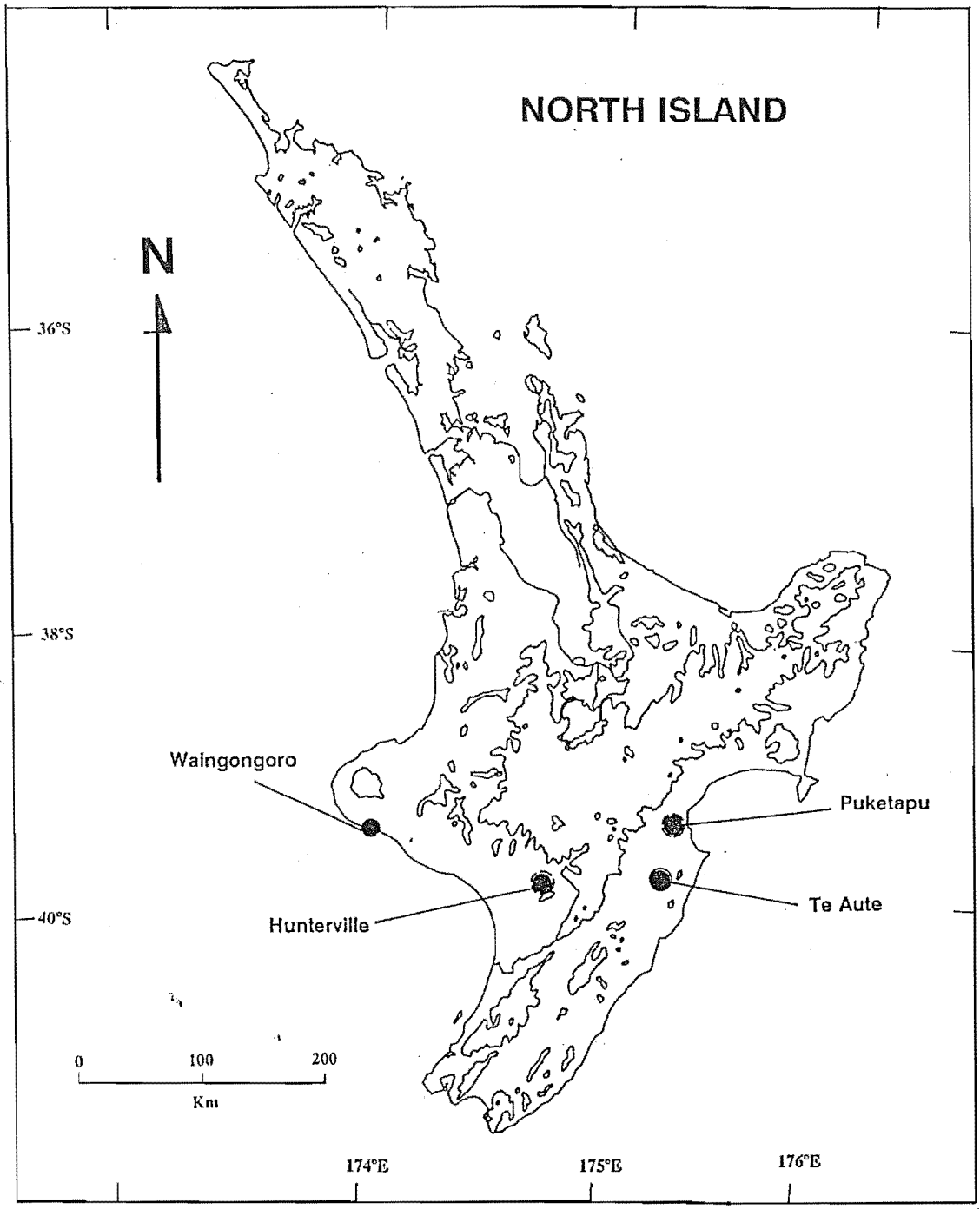

Fig. 8.34 (A, B) Distribution of sites relative to present coastline and 450 m contour: A, North Island

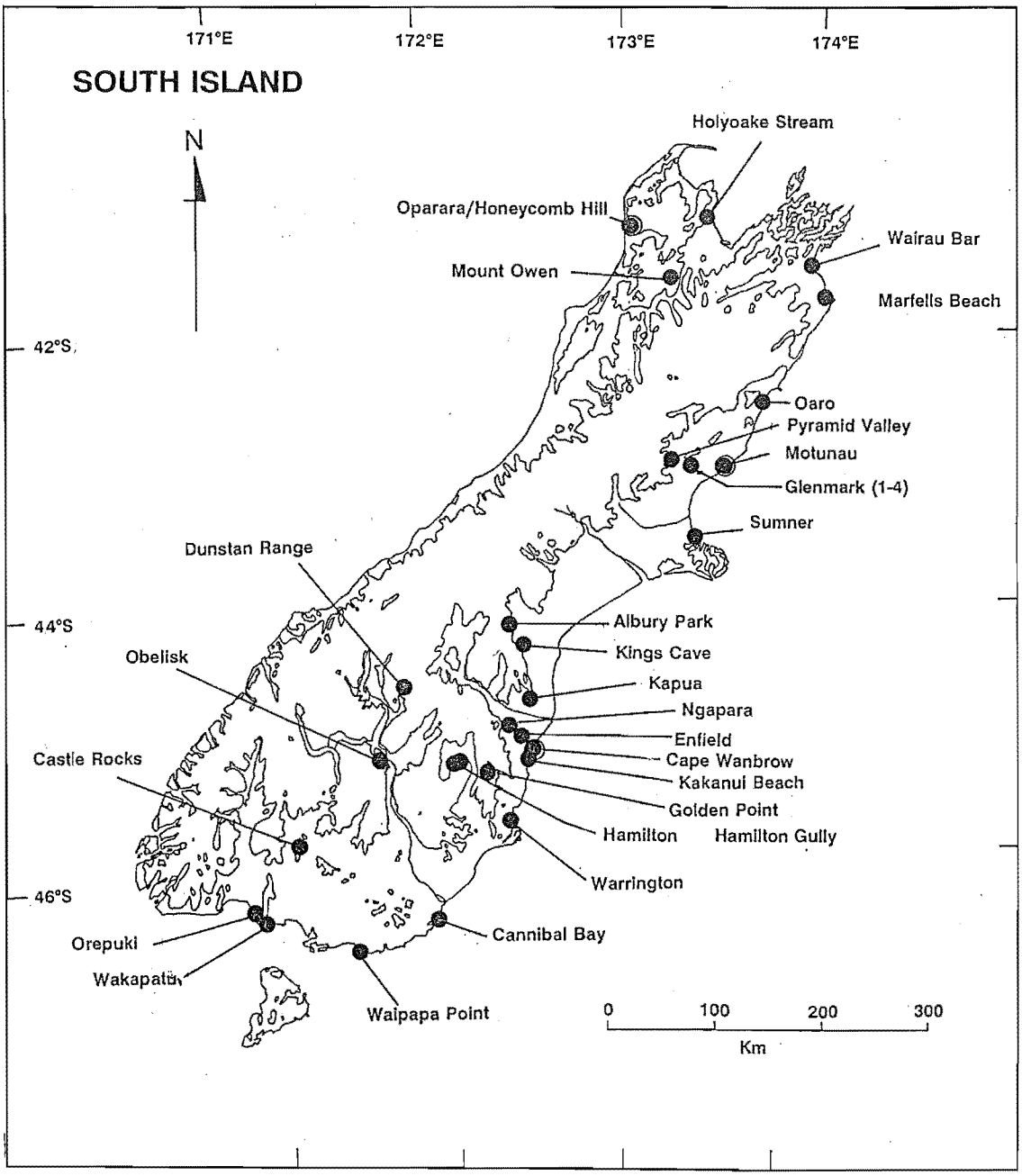

Fig. 8.34B Distribution of sites relative to present coastline and 450 m contour in the South Island.

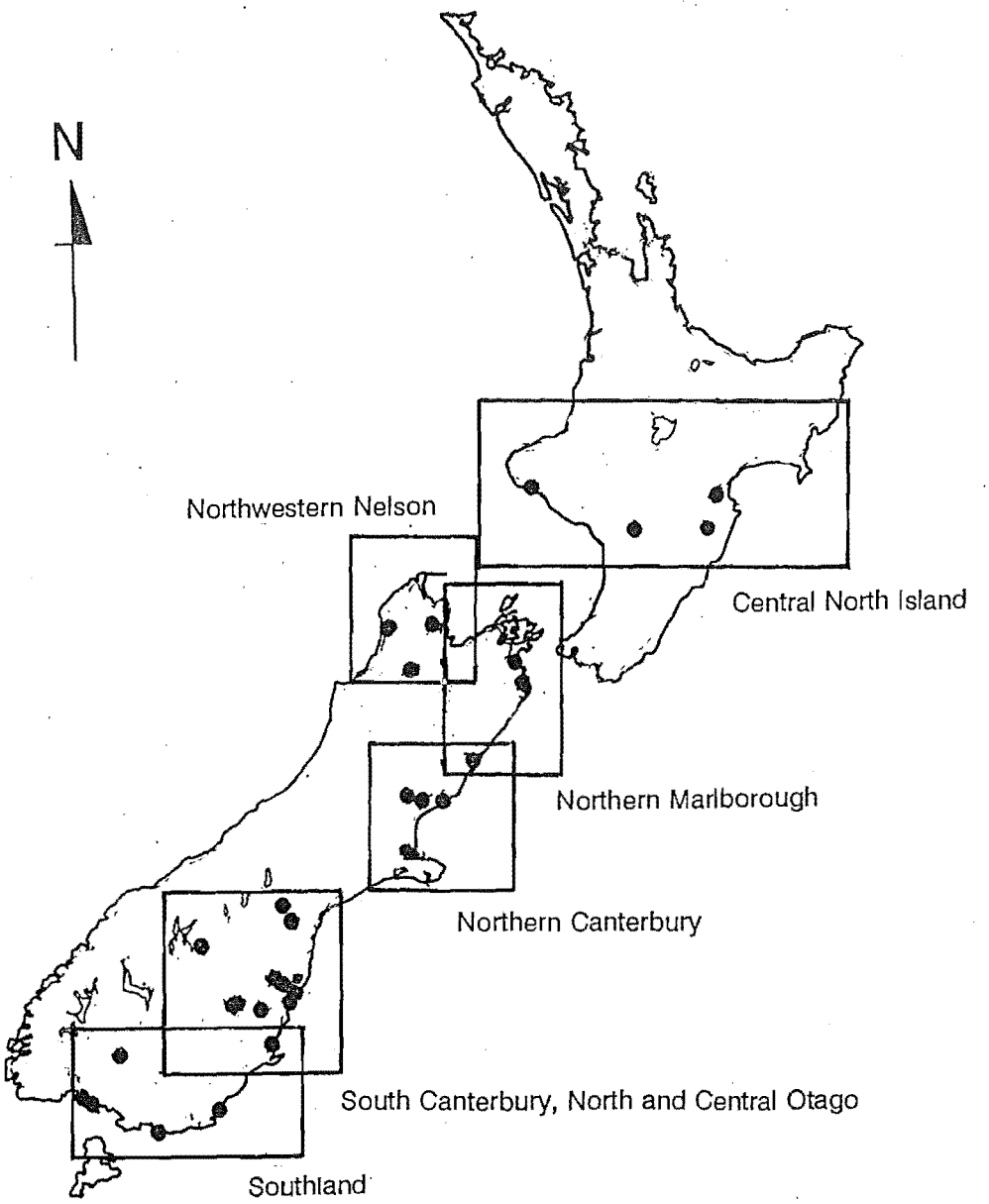

Fig. 8.35 (A-G) Distribution of localities by area: A, areas covered.

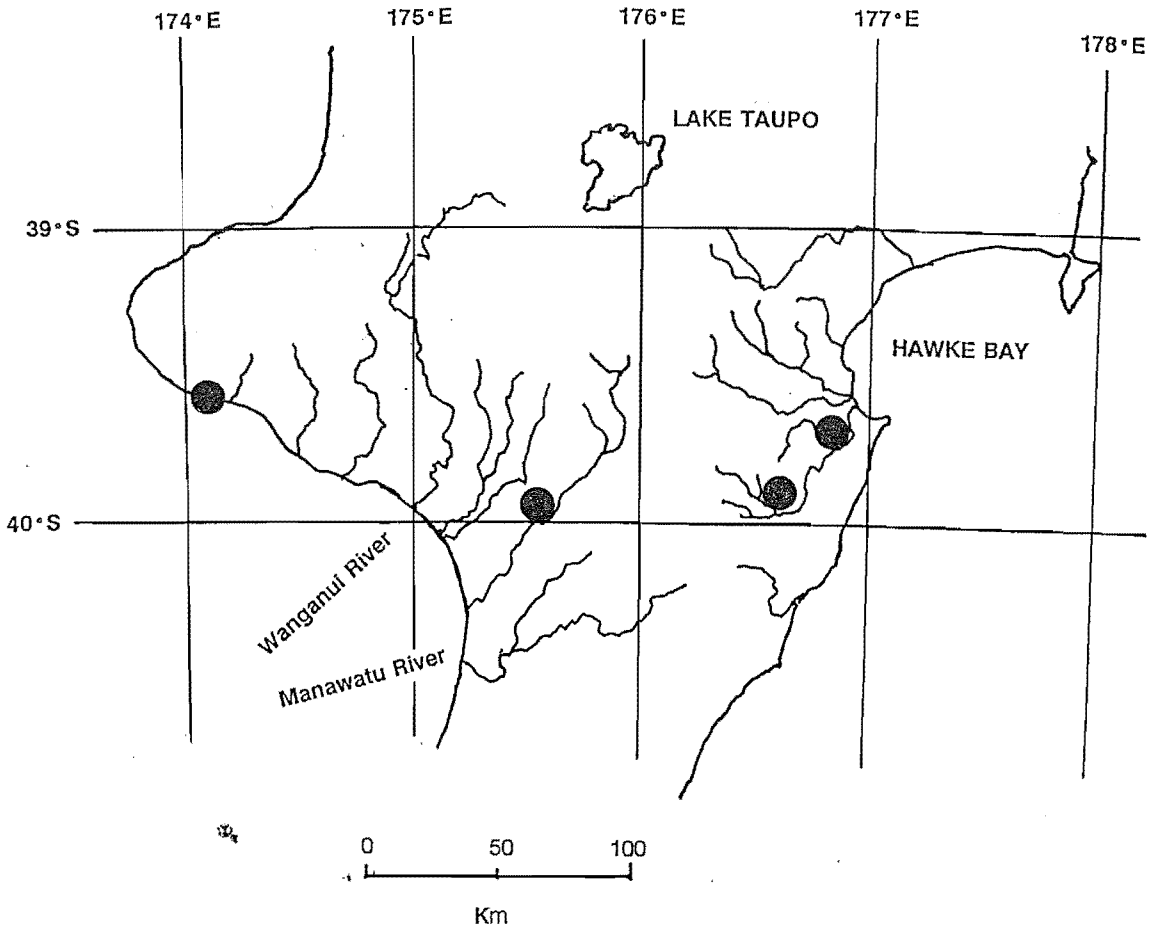

Fig. 8.35B Central North Island.

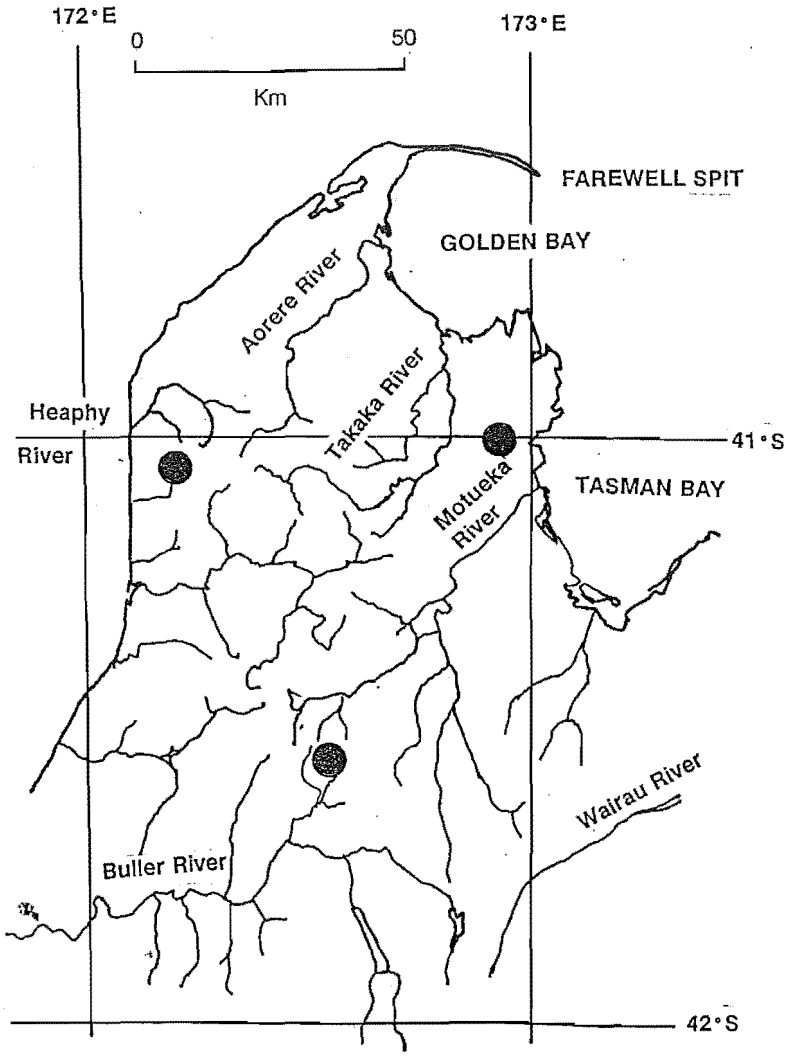

Fig. 8.35C Northwest Nelson.

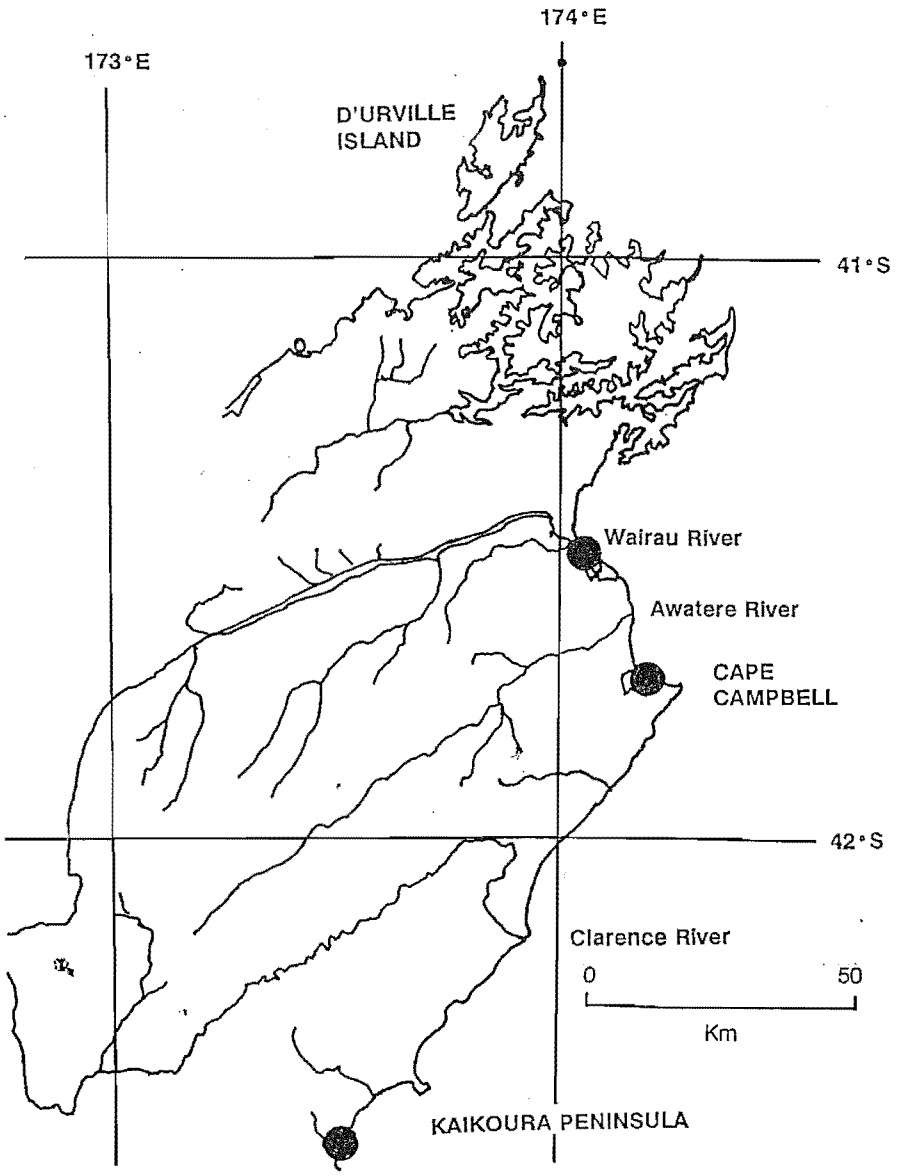

Fig. 8.35D Northern Marlborough.

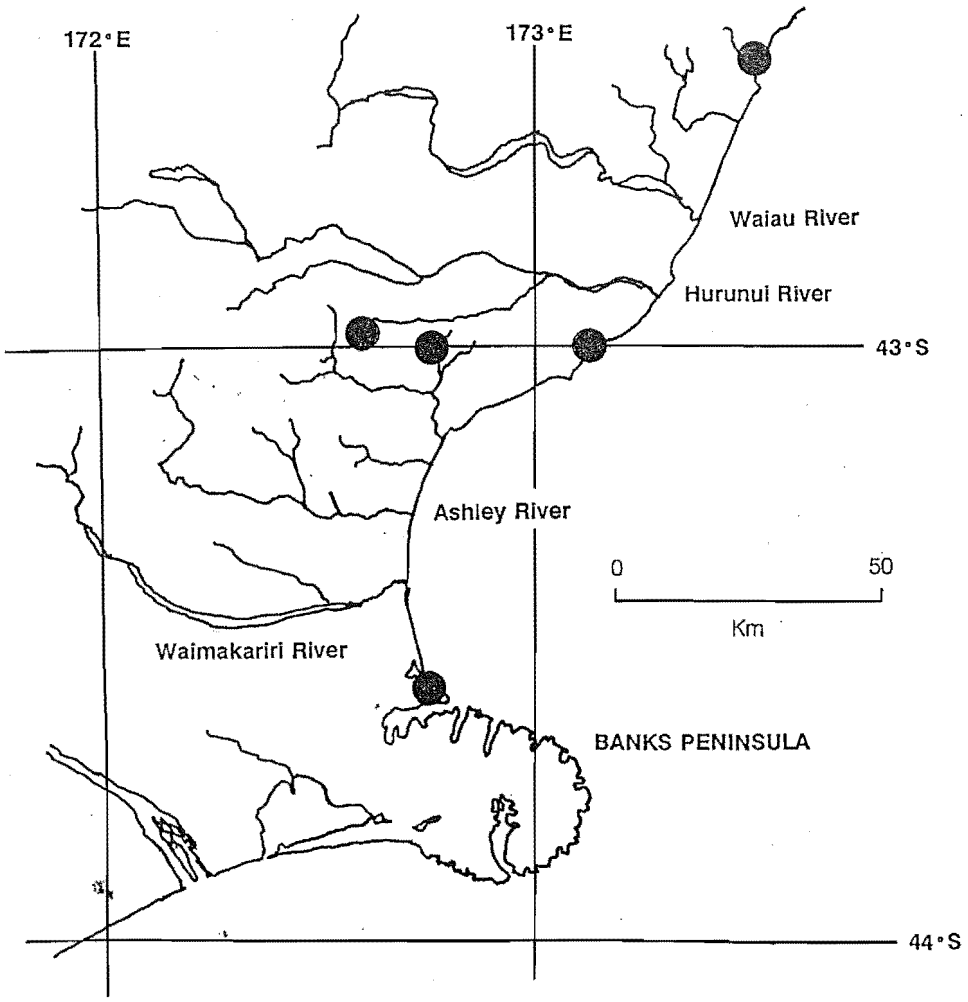

Fig. 8.35E Northern Canterbury

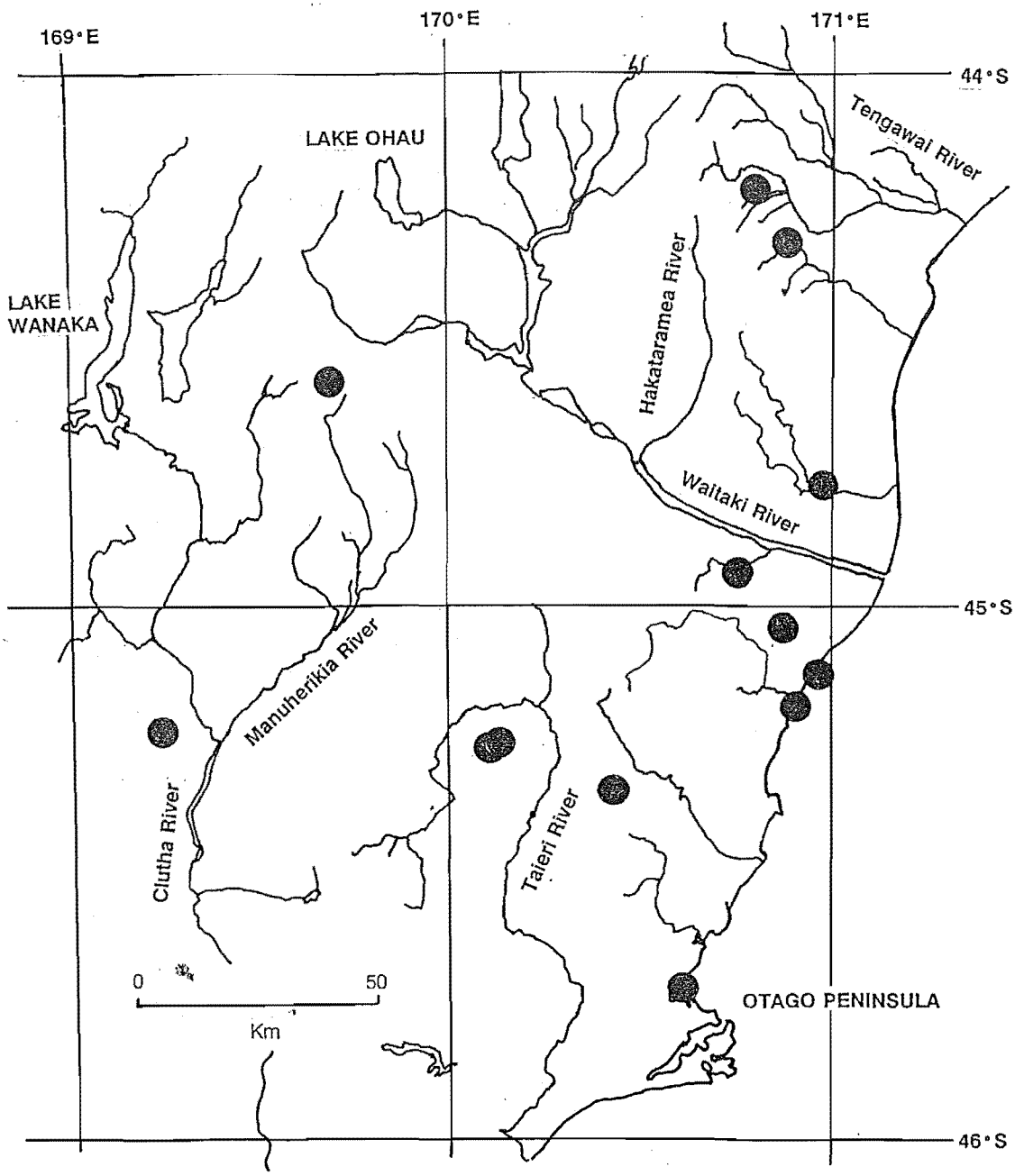

Fig. 8.35F South Canterbury, North Otago, and Central Otago.

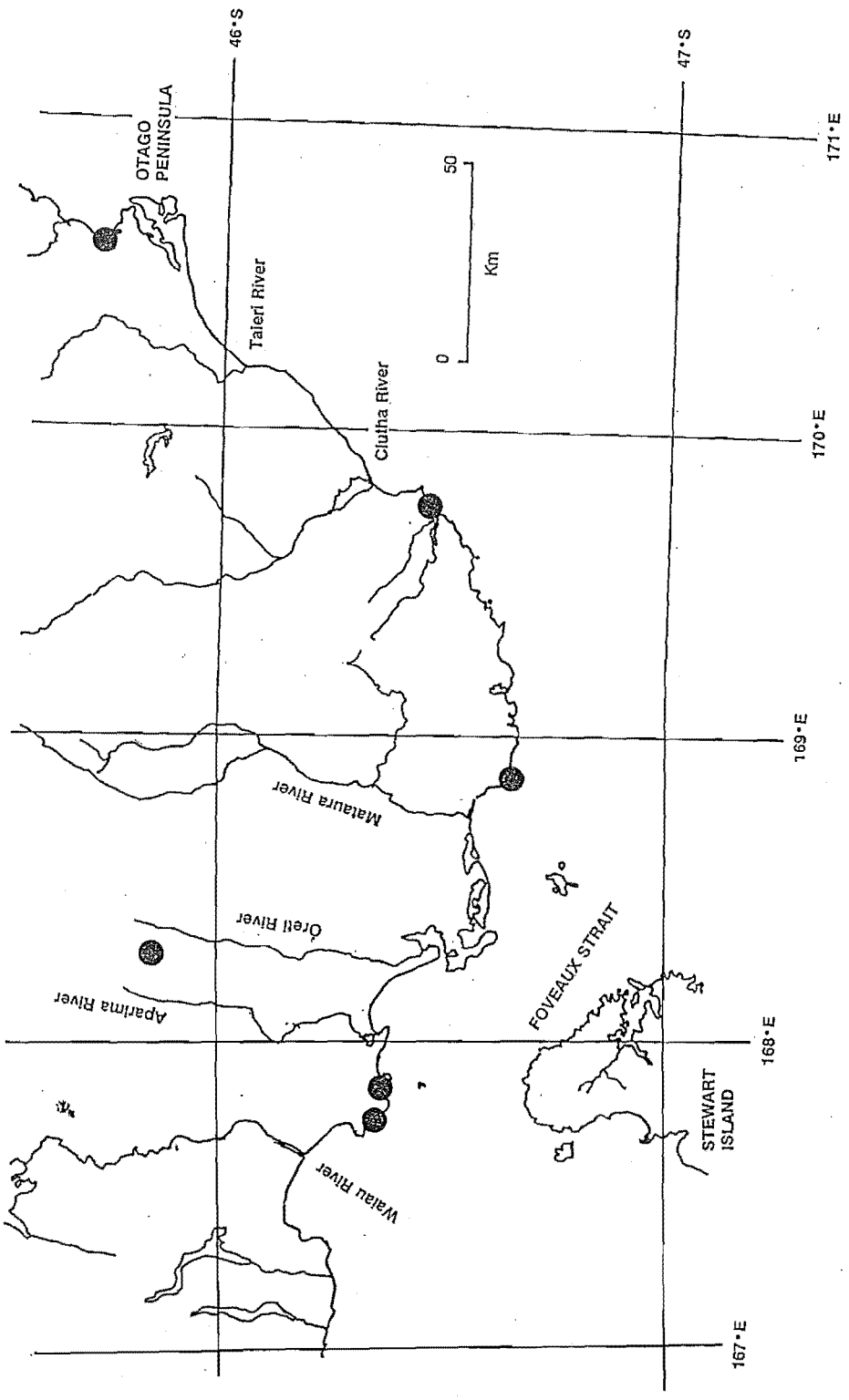

Fig. 8.35G Southland.

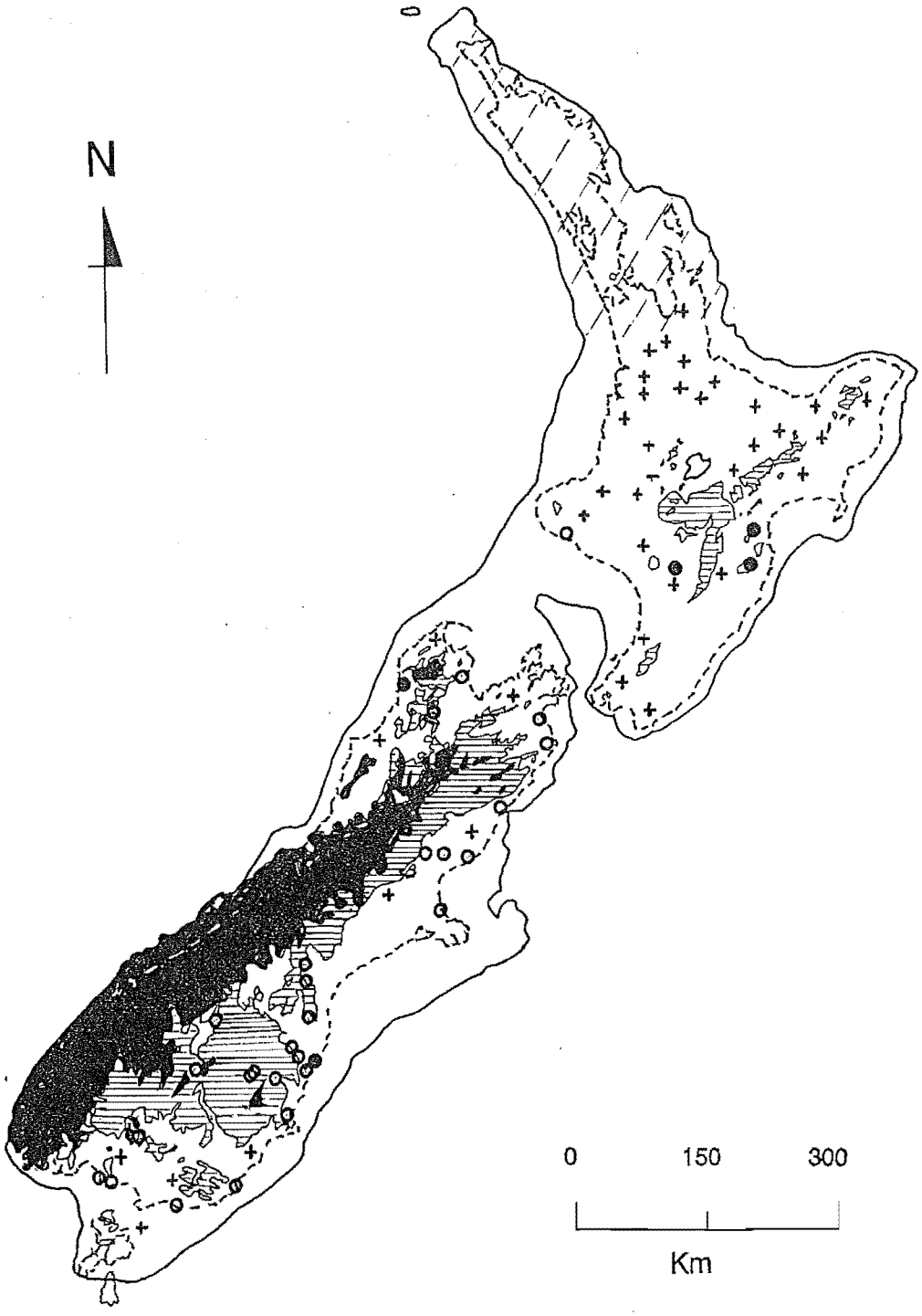

Fig. 8.36 Distribution of localities relative to assumed coastline at height of Otiran Glaciation (Pleistocene), with major vegetation patterns. Black, ice; horizontal hatching, alpine; angled hatching, uncertain, but probably more forest; remainder, grassland-shrubland; +, indicates scattered forest areas present. Dashed line indicates present coastline.

uncertainty of their altitude above this level, and the large ranges of relief over short distances in those areas.

Fig. 8.34 and Fig. 8.35 also show the distribution of eagle localities with respect to the area of New Zealand presently above 450 m. Most sites are in the lowlands; 82.9% of 34 localities, including 12 of 13 swamps, are below 500 m. The only swamp over 500 m is at Hamilton in Central Otago, on gentle slopes of the Rock and Pillar Range, above the flood plain of the Taieri River.

Fig. 8.36 shows the distribution of Pleistocene eagle sites on a reconstructed coastline and indicates the probable vegetation pattern of New Zealand during the lower sea levels of the Otiran glaciation.

Fig. 8.2-8.33 show the topography around eagle localities of Holocene age. With the exception of the area around Honeycomb Hill caves at Oparara, the topography of Pleistocene sites has been so altered by later uplift, deposition, and erosion that only general aspects of the terrain at the time of deposition can be ascertained.

As noted above, most inland localities are in areas of low to gentle relief. They are often on downland, as can be seen from the contours on Fig. 8.2-8.33. Even localities at higher altitudes, such as the Dunstan Range, and Obelisk, are on gently sloping, mature terrains. The sites with sharpest relief are Oaro and Deep Dell Creek: the first is coastal, and the second is in the bed of a steep valley cut through the subdued relief of a peneplain.

The only site in precipitous terrain is on Mount Owen (Fig. 8.18). It is at 1 600 m, on the crest of a steep ridge near the summit. However, the ridge overlooks two broad mountain basins cut into a karst terrain (Williams 1982), and so has ready visual and physical access to large areas of such terrain.

Castle Rocks fissure lies in a small rugged limestone outcrop (Hamilton 1893) but it also overlooks gently rolling terrain, and is near plains and a large swamp (Fig. 8.4).

Four localities where the sites are known or suspected to be of Pleistocene age - Cape Wanbrow, Oparara, Motunau, and Glenmark - also seem to have been in areas of low relief. The Cape Wanbrow deposits are thought to have been laid down near the shore of an estuary backed by forest (Grant-Mackie &

Scarlett 1973). The Oparara Valley is several kilometres away from the sea and was even further away during the low sea levels of the Otiran (Fig. 8.11, 8.36), but the relief was probably similar to that of the area at present (Millener 1984). The gravel and silt beds at Glenmark and Motunau (Fig. 8.7, 8.17), although dipping slightly, are generally horizontal and indicate that the lakes or swamps that produced the peats were not in steep narrow valleys.

Coastal localities are mainly in dunes or on barrier beaches. An exception is Kakanui Beach, where the coastal retreat has reached a swamp deposit that is being further eroded by high tides and storm waves. Dune material is exposed in 'blowouts' after storms, and is usually on older surfaces buried by more recent, mobile sand.

The altitudinal distribution of sites, by site type, is shown in Fig. 8.37. Only those sites separated significantly by geography or time are included. Hence, the Honeycomb Hill cave system complex, where all sites are of Pleistocene age and are grouped within a few kilometres of each other, the group of Holocene sites at Glenmark, and the group of Pleistocene sites near Cape Wanbrow, are considered to be one site.

8.3.1.2 *Distance from coast* Most sites are near the coast (Fig. 8.38); 73.5% of the sites are, or were during deposition, <30 km from the sea, and nearly 50% were within 10 km of it. Of the sites >30 km inland, three are in swamps, three in caves or under rock overhangs, and one presumed to be in a loess bed. Conditions are unknown for the other two sites. The two sites furthest inland are as far from coasts as it is possible to be in the South Island.

Few moa swamps have been excavated in the high country, and no eagle material was found at Scaife's Lagoon. Of the three inland swamp sites that have produced eagle bones, one (Albury Park) may have been associated with a cave system. The other two (Golden Point and Hamilton) were discovered during gold sluicing. Golden Point was in a streamside swamp, and Hamilton was a spring-fed pond on an open slope. Many other sluices operated in central Otago, but none is known to have exposed eagle bones. The record from Hamilton Gully may be another, but the circumstances of the find were only scantily recorded.

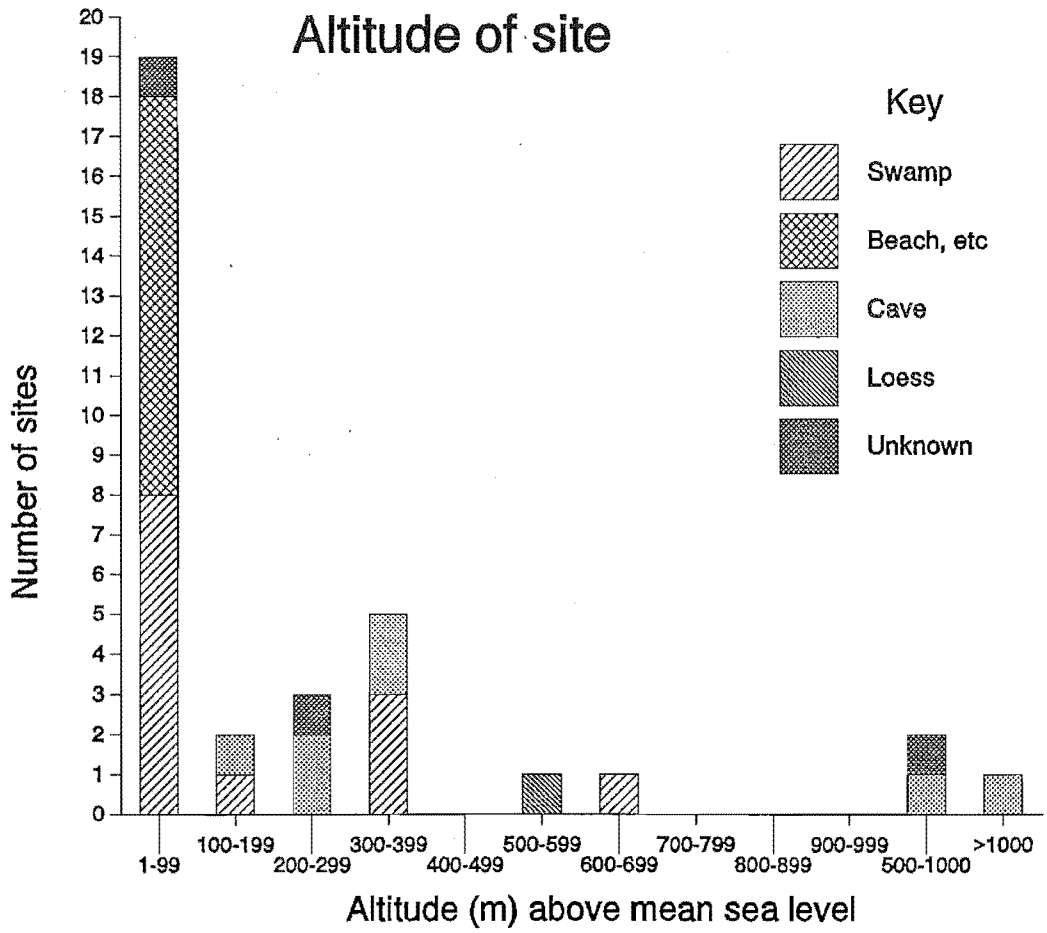

Fig. 8.37 Altitude (m) of sites above mean sea level, by site type (see Key).

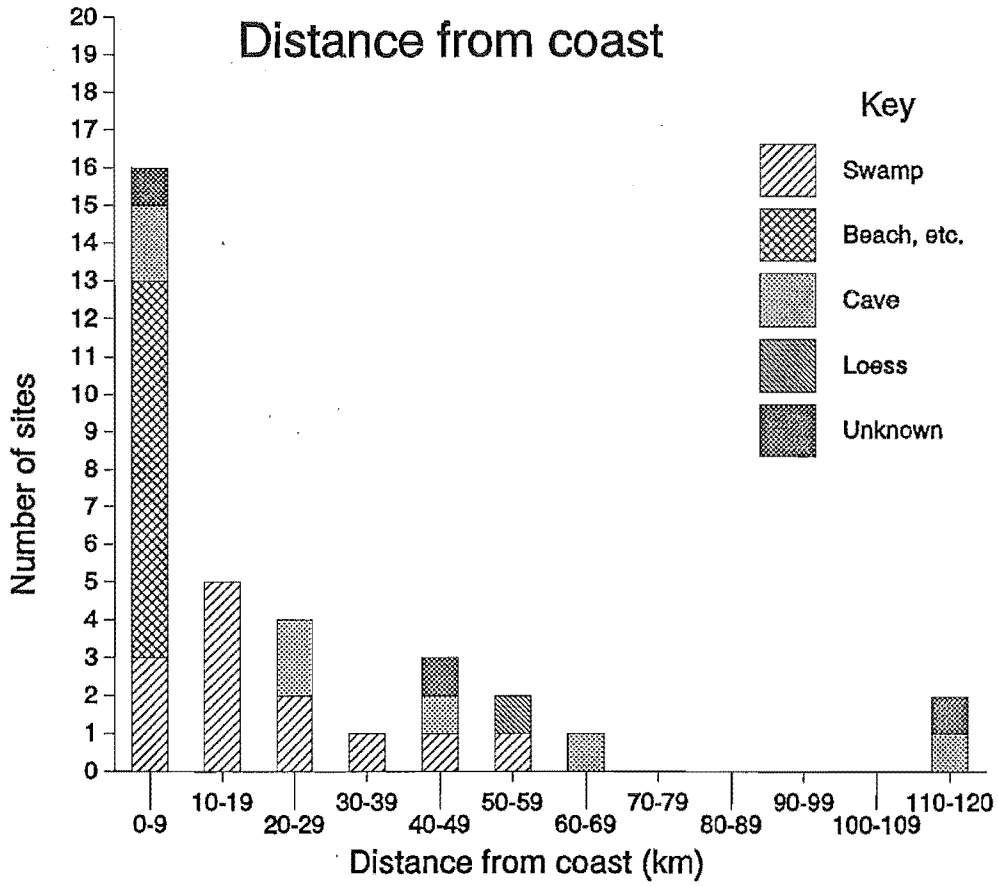

Fig. 8.38 Distance (km) of sites/localities from nearest coastline, by site type (see Key).

Many inland records were by gold prospectors or miners, who had explored most of central Otago to the main divide by the 1890s.

A rock overhang site may indicate a nest or a feeding station. The Dunstan and Obelisk records are near the glacial lakes, but whether the range extended into the valleys of the Southern Alps is unknown. However, it seems to have included most of central Otago and inland Southland (e.g, Castle Rocks).

The only inland site in the north of the South Island is on Mount Owen, southwest of Nelson. Few Quaternary sites are known in inland Marlborough, and none of these contained eagle bones. At present, it is not known how far the bird extended inland from the east coast, but it was certainly present in the karst mountains further west.

A greater abundance of sites near the coast probably does not reflect the actual distribution of Haast's Eagle. Although inland areas were prospected thoroughly by miners over many years, the few sites discovered probably indicates a scarcity of suitable places where fossilisation could occur rather than a lack of birds. Sites are scattered over thousands of square kilometres of similar terrain, where suitable habitat for possible prey was widespread (Anderson 1983). The known sites are unlikely to have been the only inland places where eagles were found.

8.3.1.3 *Rainfall and soils* Holocene sites are mainly in areas where the present rainfall is below 800 mm, and only the Mount Owen site is outside the 1200 mm isohyet (Fig. 8.39). The 800 mm isohyet also contains most of the brown-grey and yellow-grey soils that developed under drier vegetation types on flat to rolling hill country (Fig 8.40). Temperatures were, so far as is known, likely to have been at least seasonally equable in most areas where eagle remains have been found (Fig. 8.41).

Little is known about precipitation patterns during the Otiran glacial maximum 22 000 to 14 000 years BP, but McGlone (1988) has suggested that precipitation may have been somewhat lower than at present. Snowline was 800 to 830 m below its present level in the central Southern Alps (Porter 1975) and on the major volcanoes of the central North Island plateau. The South Island

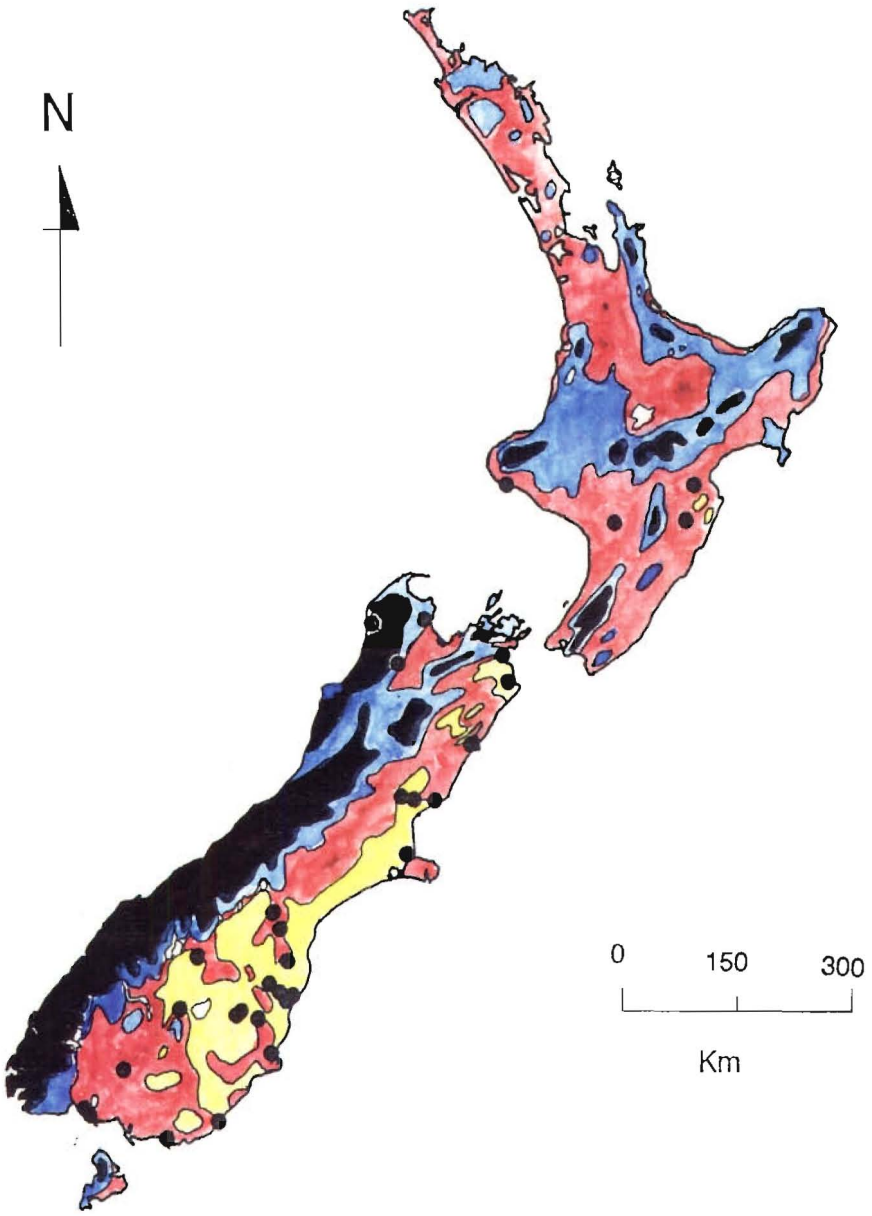

Fig. 8.39 Distribution of localities relative to present precipitation pattern (isohyets) (after Coulter 1970). Open <400 mm; yellow 400-800 mm; red 800-1600; blue 1600-3200; black >3200 mm.

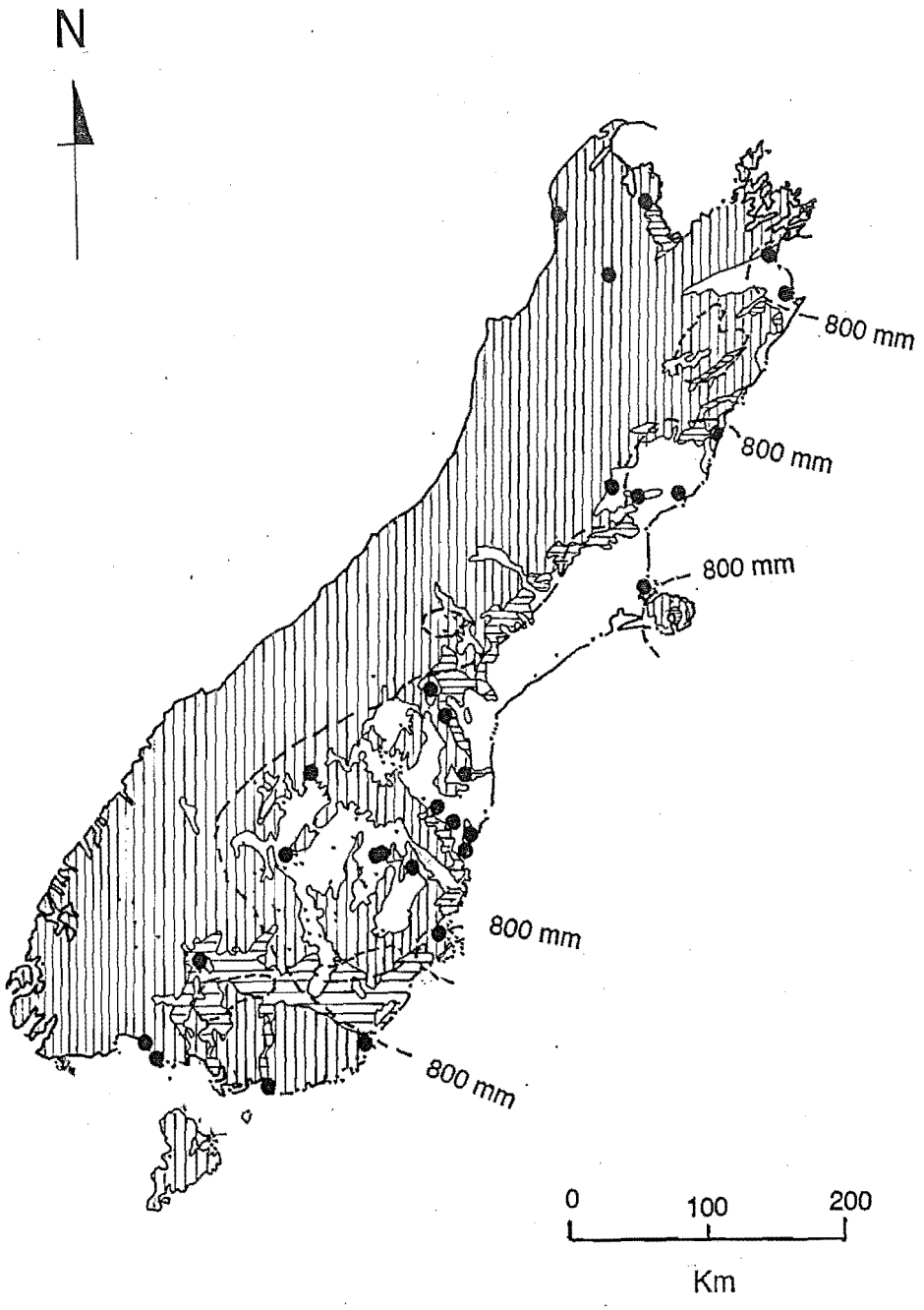

Fig. 8.40 Distribution of eagle localities relative to major soil types of the South Island, in relation to the 800 mm isohyet (after Anderson 1990). Broken line, 800 mm isohyet; vertical hatching, yellow-brown earths, podzols, and organic soils; horizontal hatching yellow-grey earths in higher rainfall regimes, and recent soils; open, brown-grey and yellow-grey earths and recent soils.

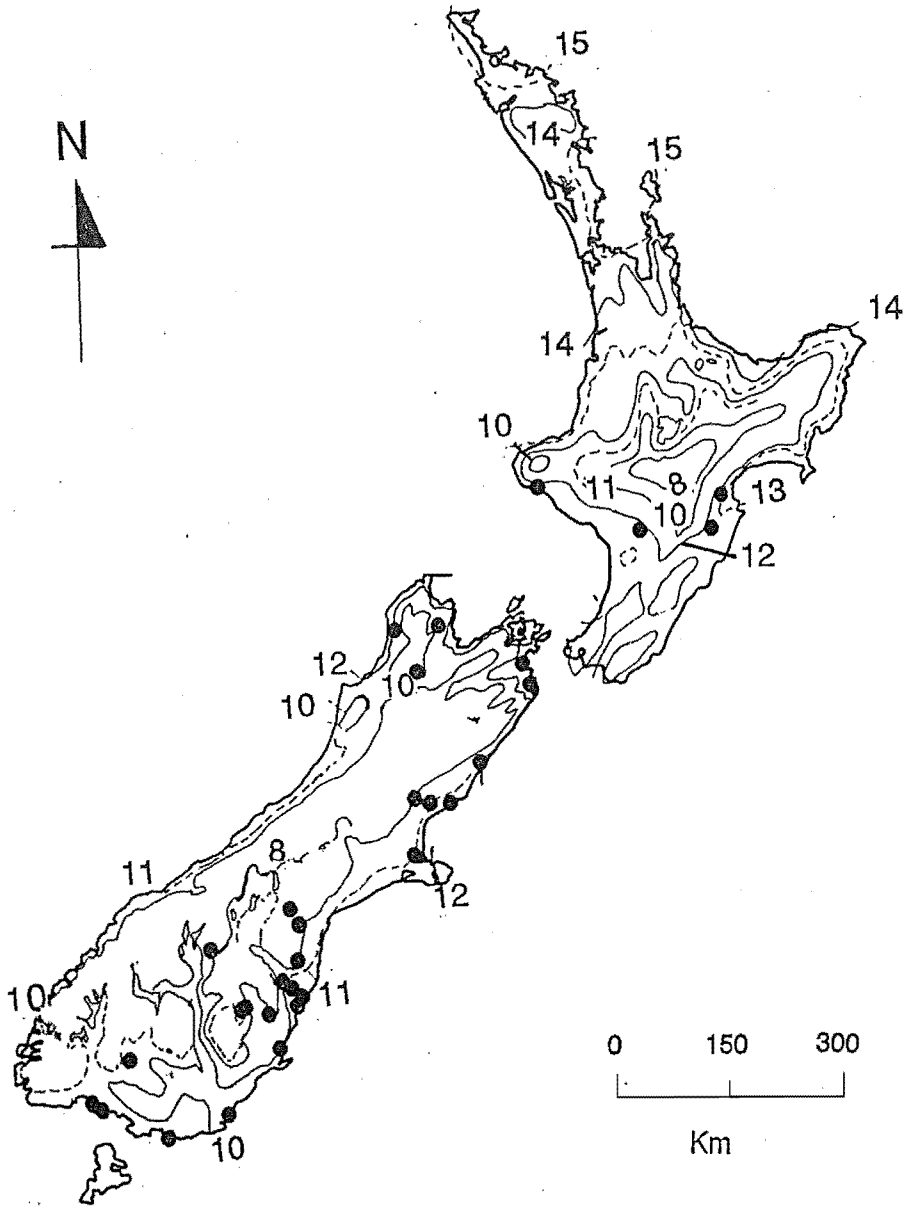

Fig. 8.41 Distribution of eagle localities relative to present mean annual temperature (max + min/2, °C) (after Coulter 1970).

high country may have been snow-covered for five months of the year during the Otiran glacial maximum (Soons 1979), and some lake basins in the North Island had lower water levels than at present (McGlone & Topping 1983), suggesting a lower precipitation rate.

Climatic conditions during the period when the Cape Wanbrow deposits were being formed were mild and moist enough to support forest vegetation on the east coast of the South Island. Grant-Mackie & Scarlett (1973) suggested that sea temperatures near Oamaru were probably the same or slightly higher than at present[1]. Climates around Glenmark and Motunau allowed the growth of forest - at least two forests grew and were destroyed at Motunau (McKay 1882) - and the formation of peat (Haast 1879; McKay 1882).

Fossil sites containing eagle material are rare in high rainfall areas today (Fig. 8.39), and therefore exhibit a similar pattern to that say in the distribution of Pleistocene age sites. Today, the typical natural vegetation in high rainfall lowland areas is tall podocarp-hardwood rain forest, or mixed *Nothofagus*-podocarp rain forest. Pollen data suggest that this was true throughout the Holocene (McGlone 1983, 1988, 1989). These forests occur on yellow-brown earths and podzols whose distribution is mainly outside the known Holocene distribution of Haast's Eagle.

The apparent absence of eagles from lowland high rainfall areas does not seem to be an artefact of the poor preservation qualities of acid soils. Diverse fossil avifaunas are known from rain forest areas: from caves in the Waikato (Millener & Templer 1981; Worthy 1984), on the West Coast of the South Island (Millener 1980), and in lake swamps such as Poukawa (Horn 1983).

8.3.1.4 *Vegetation and palaeovegetation* General patterns of vegetation (based mainly on palynological evidence) are compared with the known distribution of eagle and other sites in Fig. 8.36 and Fig. 8.42. Many sites, however, contain direct information on the vegetation present in their vicinity during deposition.

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[1]Probably during the Oturian Interglacial of the Haweran Series, although the date is uncertain.

This information ranges from detailed analyses of microfossils to macrofossils recovered from the sediments. General comments on the macrofossils are included in the site descriptions (see above); for many sites, this is the only information because the site was destroyed and no plant material was preserved. For a few there is copious information, and this is summarised in Table 8.2.

Of all sites, swamps are probably the most important sources of direct evidence on eagle habitat. Plant macrofossils from the surrounding vegetation are usually present in the deposit. These and a sample of the avifauna coexisting with the eagles, which together provide more data on the ecology of the eagle than does the mere presence of its remains.

For the period of the latest maximum of the Otiran glaciation (22 000-14 000 years BP), eagle sites are known only from areas of grassland-shrubland with scattered areas of forest (Fig. 8.36). No sites of this age are known from the east and south of the South Island. McGlone (1988) suggested that patches of forest, or at least woody vegetation were widespread in warmer sites, especially those sheltered from cold dry winds from the south and west. The material from Te Aute was associated with remains of woody vegetation (Table 8.2; Hamilton 1889). Worthy & Mildenhall (1989) provided floral and faunal evidence that the vegetation around the Oparara sites was subalpine shrubland and montane forest.

As with the climate, vegetation patterns for the warmer period before the last maximum, and for the last (Oturian) interglacial, are unclear. However, the sites at Cape Wanbrow contained faunal evidence for the presence of forest in the form of forest passerine birds and two species of damp forest landsnails (Grant-Mackie & Scarlett 1973).

From about 14 000 years BP, reforestation proceeded rapidly in the North island and in the northwest of the South Island, although more slowly in the area around the present Cook Strait that were more exposed to strong westerly and southerly winds (McGlone 1988). After about 10 000 BP, vegetation patterns apparently changed only in minor details from those found 3 000 years ago (Fig. 8.42). All but two South Island sites were in or near areas of drier podocarp-hardwood forests with mosaics of shrubland, swamps, and riparian and basin

Table 8.2 Vegetation at or near eagle sites (upper section) or sites without eagle (lower section) during period of fossil deposition. Age: P, Pleistocene; H, Holocene. Vegetation types after Worthy (1990). ?, unknown or doubtful. Continued on next page. Sources: 1, McGlone (1989); 2, Worthy & Mildenhall (1989); 3, Anderson (1982); 4, Haast (1879); 5, McKay (1882); 6, Hamilton (1904); 7, Grant-Mackie & Scarlett (1973); 8, Burrows (1989); 9, Hamilton (1889); 10, Bussell (1988); 11, Brown (1981); 12, Worthy (1990); 13, Yaldwyn (1958); 14, Millener & Templer (1981); 15, Horn (1983); 16, McGlone (1988); 17, Coster (1983); 18, Dodson *et al.* (1988).

Site	Age	Vegetation	Evidence	Source
Albury Park	H	Forest	Recent vegetation	1
AR 144	P	Mosaic forest; subalpine shrubland	Pollen	2
Cannibal Bay	H	Coastal forest; lowland forest	Recent vegetation	P
Castle Rocks	H	Lowland forest	Recent vegetation	1
Dunstan Range	H?	Forest	Fossil logs; forest dimples	3
E entrance	P	Mosaic forest; subalpine shrubland	Pollen	2
Eagle Roost	P	Mosaic forest; subalpine shrubland	Pollen	2
Enfield	H	Forest?	Pollen	1
Glenmark Creek	P	Forest?	Pollen?	1
Glenmark/East	H	Forest	Logs and branches	4
Glenmark/West	H	Forest	Logs and branches	4
Glenmark Creek 2	P	Forest?	Pollen?	1
Golden Point	?	Forest?	Fossil logs; forest dimples	3
Graveyard	P	Mosaic forest; subalpine shrubland	Pollen	2
	H	Lowland forest	Pollen	2
Hamilton Swamp	H	Forest	Fossil logs; forest dimples	2
Hamilton Gully	?	Forest?	Fossil logs; forest dimples	3
His Cave	P	Mosaic forest; subalpine shrubland	Pollen	2
Hives extension	P	Mosaic forest; subalpine shrubland	Pollen	2
Holyoake Stream	H/P	Mosaic forest/subalpine shrubland?	Recent vegetation	P
Hunterville	P?	?		
Kakanui Beach	H	Coastal forest	Recent vegetation	1
Kapua	H	Forest; shrubland	Pollen	1
Kings Cave	H	Forest	Pollen	1

Table 8.2 continued Vegetation at or near eagle sites (upper section) or sites without eagle (lower section) during period of fossil deposition. Age: P, Pleistocene; H, Holocene. Vegetation types after Worthy (1990). ?, unknown or doubtful. Lower six localities (below line) have large fossil avifaunas, but contained no eagle bones. Sources: 1, McGlone (1989); 2, Worthy & Mildenhall (1989); 3, Anderson (1982); 4, Haast (1879); 5, McKay (1882); 6, Hamilton (1904); 7, Grant-Mackie & Scarlett (1973); 8, Burrows (1989); 9, Hamilton (1889); 10, Bussell (1988); 11, Brown (1981); 12, Worthy (1990); 13, Yaldwyn (1958); 14, Millener & Templer (1981); 15, Horn (1983); 16, McGlone (1988); 17, Coster (1983); 18, Dodson *et al.* (1988).

Site	Age	Vegetation	Evidence	Source
Marfells Beach	H	Coastal forest; shrubland	Pollen	1
Motunau	P	Forest	Fossil logs and stumps	5
Mount Owen	H	Subalpine grassland/forest	Recent vegetation	P
Ngapara	H	Forest	Recent vegetation	6
Oaro	H?	Coastal forest	Recent vegetation	P
Obelisk Range	H?	Forest	Fossil logs; pollen	3
Old Rifle Butts	P	Forest	Mollusc shells	7
Orepuki	H	Coastal and lowland forest	Recent vegetation	P
Puketapu	?	?		
Pyramid Valley	H	Forest	Macrofossils; fruit; wood	8
Shirley Creek	P	Forest	Molluscs; vertebrates	7
Sumner	H	Coastal and lowland forest	Recent vegetation	
Te Aute no. 2	P	Forest	Fossil wood; seeds	9
Waingongoro	H	Coastal forest	Pollen; fossil stumps	10
Waipapa Point	H	Coastal forest; shrubland	Recent vegetation	
Wairau Bar	H	Coastal forest; shrubland	Recent vegetation; fossil logs	11
Wakapatu	H	Coastal forest; shrubland	Recent vegetation	
Warrington	H	Coastal forest; shrubland	Recent vegetation	
Makirikiri	H	Lowland forest	Pollen	10,12
Martinborough	H	Lowland forest	Invertebrates	13
Metro Cave area	H	Lowland forest	Recent vegetation	P
Paryphanta	H/P?	Lowland forest	Pollen	14
Lake Poukawa	H	Lowland forest	Pollen	15,16
Tokerau/Far North	H	Lowland forest; scrub/shrub	Pollen; fossil wood	17,18

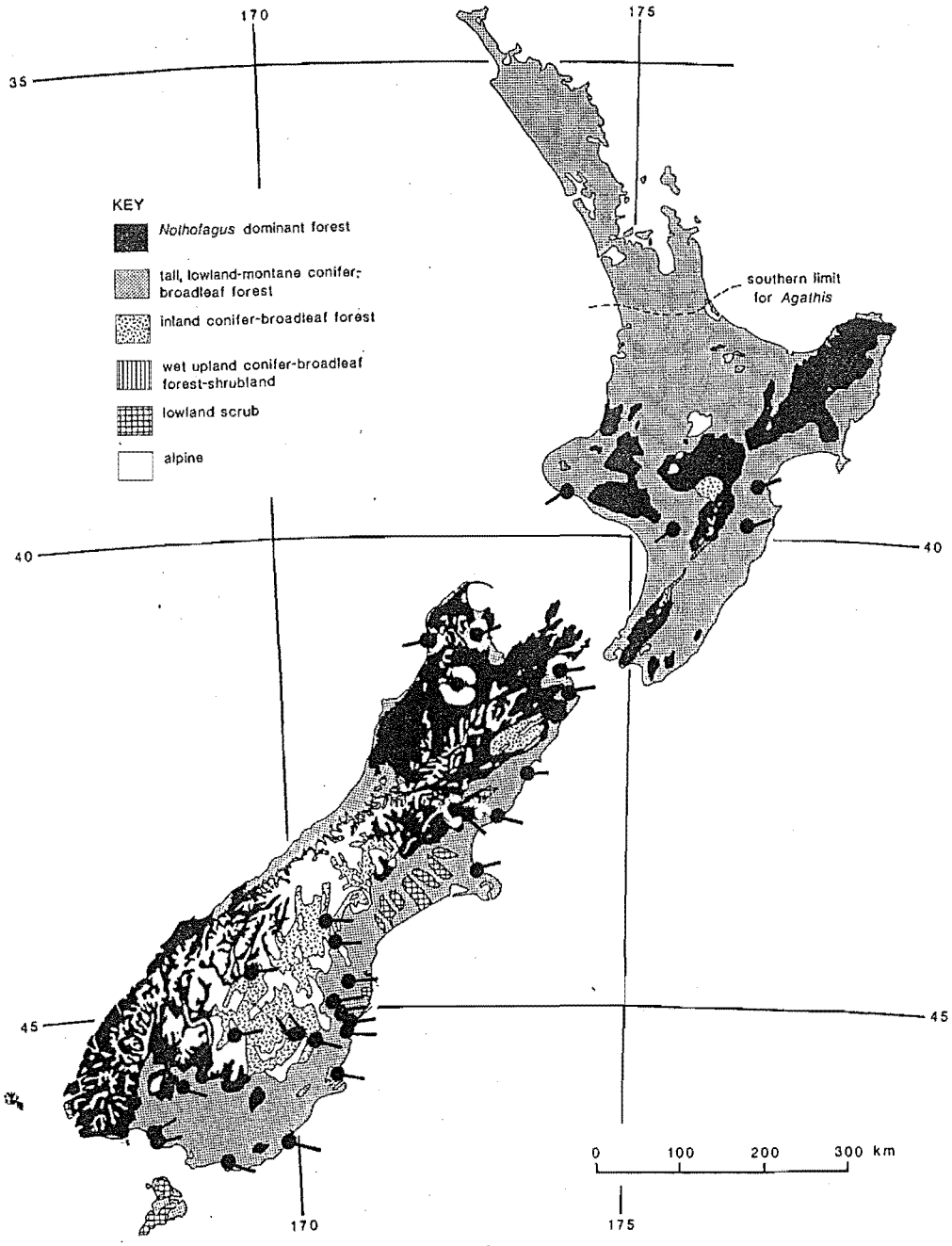

Fig. 8.42 Distribution of Holocene-dated eagle localities relative to vegetation pattern at 3 000 years Before Present (after McGlone 1989).

grasslands (Fig. 8.42). Of the two exceptions, Mount Owen was, and is, in subalpine grassland and herbfield, and Holyoake Stream was in wetter coastal podocarp-hardwood-*Nothofagus* forest.

All the drier forest sites were in areas that had been deforested by Polynesian fires between 400 and 800 years BP (McGlone 1989). The distribution of Holocene sites is almost entirely outside areas of forest remaining in 1840 AD, near the start of the European era (Fig. 8.43).

Pollen and macrofossils indicate that forest and forest-scrub ecotones, rather than grassland, savanna woodland, or lowland wet rain forest, were the commonest vegetation near eagle sites (Table 8.2; Fig. 8.42).

8.3.1.5 *Geology* Fourteen sites (33%) are on karst or in areas of calcareous rocks (Fig. 8.44), a not unexpected finding because of the favourable conditions of preservation characteristic of calcareous sediments. However, the correlation between rock type and presence of eagle fossils is not so tight as to support the suggestion that the location of sites mirrors the location of karst. However, 67% of sites are on non-calcareous rocks, such as schists, or in silts or dunes (Table 8.1). In addition, many karst sites with diverse fossil avifaunas do not contain eagle material, even though they are otherwise similar to sites that do.

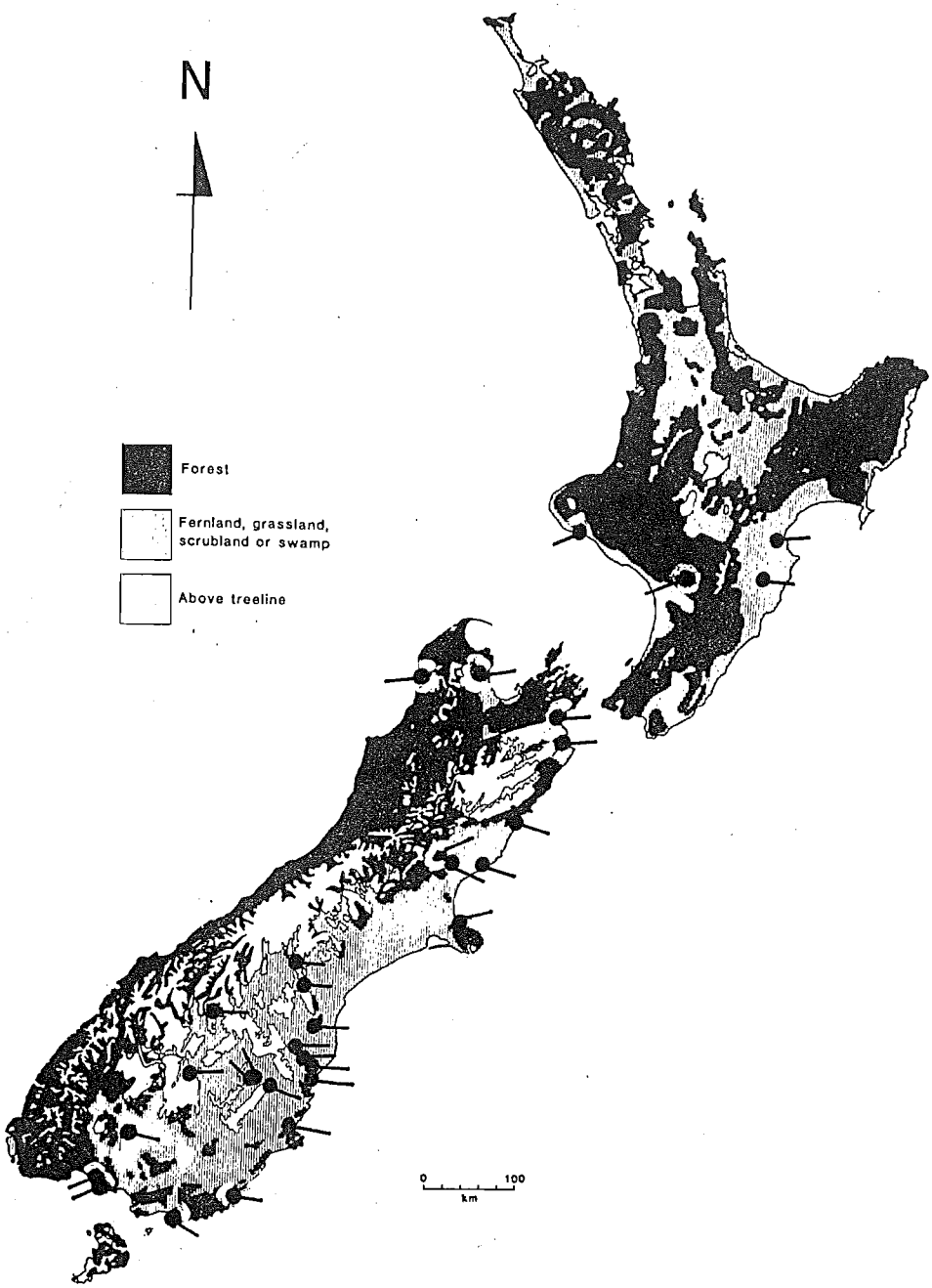

Fig. 8.43 Distribution of Holocene-dated eagle localities relative to vegetation pattern at 1840 AD (after McGlone 1989).

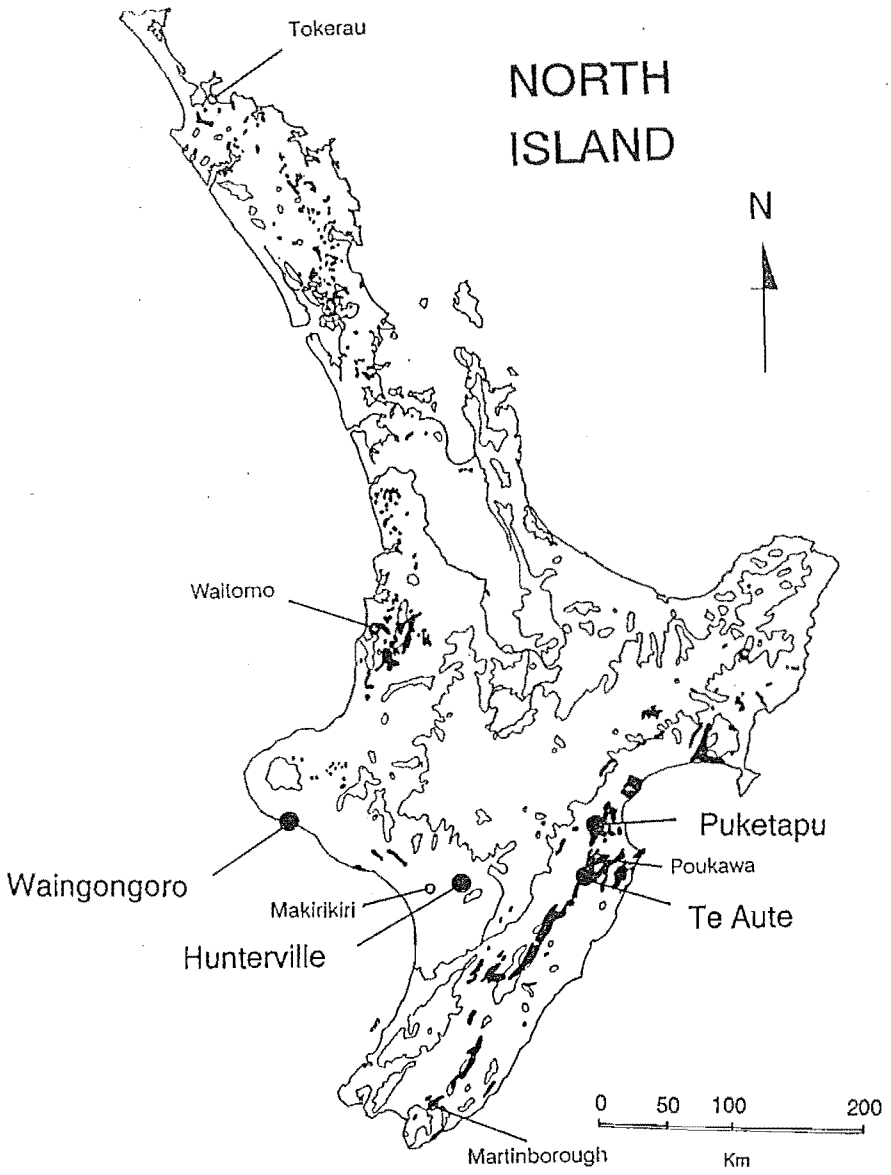

Fig. 8.44 (A, B) Distribution of Recent fossil bird localities relative to the distribution of karst areas, and other major exposures of calcareous rocks. Filled circles, eagle sites; open circles, sites lacking eagles: A, North Island. (After Williams, in Soons (1982)).

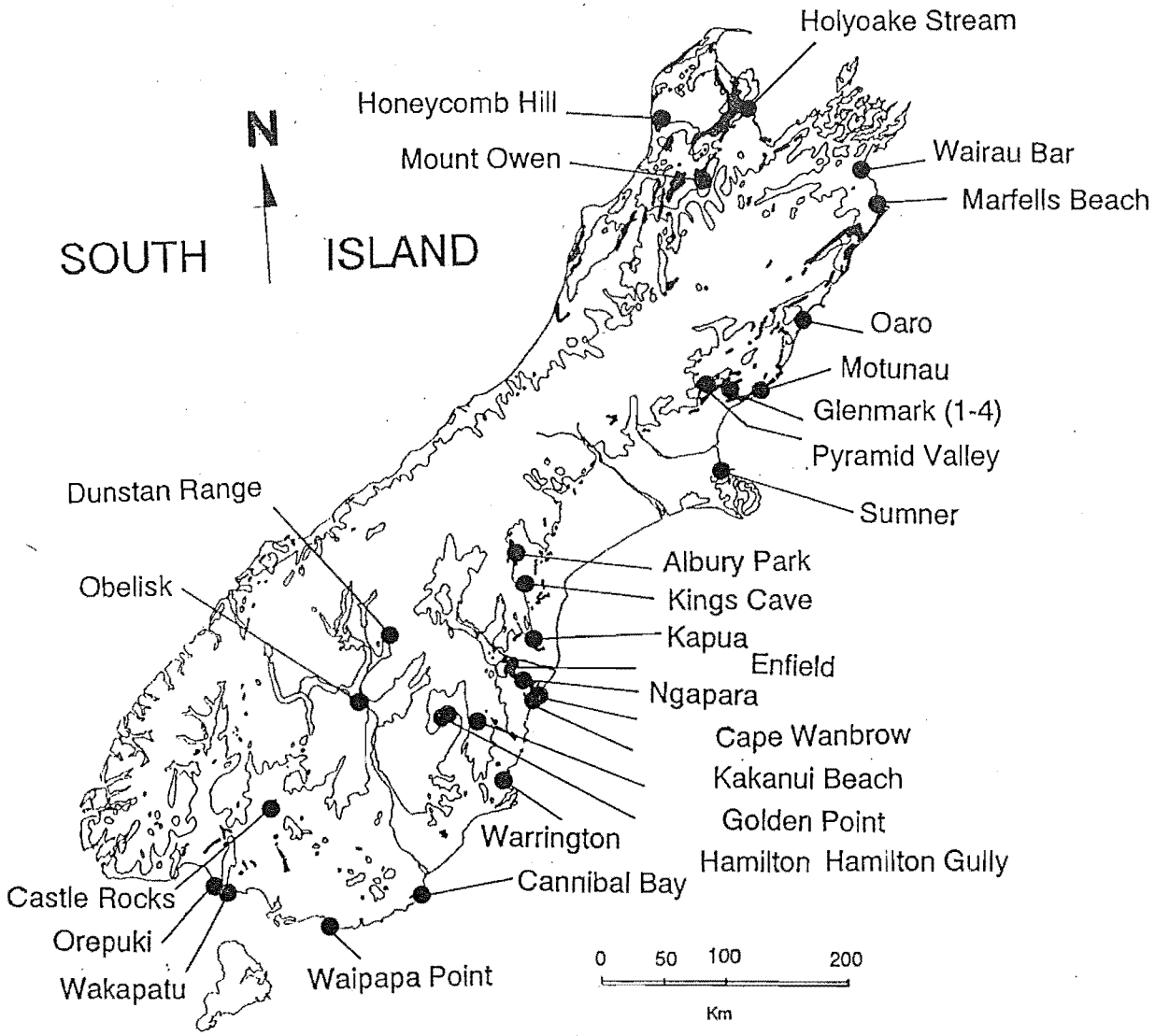

Fig. 8.44B Distribution of Recent fossil bird localities in the South Island relative to the distribution of karst areas, and other major exposures of calcareous rocks. Filled circles, eagle sites; open circles, sites lacking eagles. (After Williams, in Soons (1982).

8.4 AGE OF DEPOSITS

8.4.1 General

The conventions used here for broad geological age were outlined in the General Introduction. According to those criteria, most eagle sites are of Holocene age, but 12 or 13 are of Pleistocene age (Table 8.1). Six of the Pleistocene sites are in or near the Honeycomb Hill cave system in northwest Nelson.

Assignments were based on either available ^{14}C dates (Table 8.3), or events such as Holocene dune formation. If the site had been destroyed, a subjective assessment was made based on the known age of apparently similar sites.

Only two radioisotope (^{14}C) dates are based directly on eagle bone. Dates on small or organically depleted samples became feasible only with the development of tandem accelerator mass spectroscopy (TAMS) techniques in the 1980s. The relatively small size and apparent rarity of eagle bones precluded their sacrifice in the amounts needed for a conventional emission count ^{14}C date. TAMS dating, which requires milligram amounts of bone, has allowed the direct dating of elements from a much wider range of taxa than was possible with the conventional technique (Martin 1987).

Before TAMS dating became available, the ages of eagle bones and other taxa in fossil faunas from New Zealand were estimated by stratigraphic association with datable material, usually moa bone collagen or charcoal. The possibility of reworking of deposits, and the presence of charcoal with 'inbuilt age', reduced the value of many such dates by association.

^{14}C dates from natural fossil sites containing eagle material ranged from >35 900±1 700 to 2 160±110 years BP (Old T½), and were mostly based on samples of moa bone. The two dates derived directly from eagle bone were 15 530±200 (NZA 361) and 2 160±110 (NZA 905) years BP.

Dates for swamps in the coastal strip and in the downlands and ranges east of the Southern Alps suggested that most, if not all, were formed during the Holocene (Table 8.3). Dates on moa bone from Pyramid Valley were similar (Burrows 1989; McCulloch & Trotter 1979), and suggest that this site at least operated as a trap for only a relatively short period. Kapua and Kakanui Beach

swamp sites were taken as being of Holocene age by analogy with the dated swamp at nearby Enfield.

Worthy (1987) presented stratigraphic and faunal evidence that Te Aute may be considerably older, perhaps dating from the Otiran. The Puketapu site nearby, about which little has been recorded, may also be of Pleistocene age.

No dates were available for the fissure and cave fills at Castle Rocks, Holyoake Stream, Kings Cave, or Ngapara. However, on stratigraphic and geomorphological grounds, all are probably younger than 14 000 years. Worthy (1988) suggested that the Castle Rocks fissure deposit should be dated at 2 000-3 000 years BP because of its location. Moa bone from a pothole near Martinborough, in the southern North Island (Yaldwyn 1956, 1958), gave a date of 1 470±50 years BP (NZ4150, McCulloch & Trotter 1979). The Holyoake Stream fissure deposit is unlikely to be substantially older. Bone was visible on the surface from outside the fissure, and the eagle cranium was surface collected (H Belton, pers. comm.). As noted in section 8.2.2.10, it now seems likely that the Holyoake Stream site actually refers to a deposit in Hawkes Cave, Takaka Hill. If so, then the date is likely to be early Holocene at the latest, and probably at least 10 000 years BP. Faunas from at least two distinct periods are preserved in the deposits; the eagle specimen was associated most closely with taxa characteristic of the area during the Otiran glaciation (pers. obs., T H Worthy, pers comm.).

According to Worthy (1988: 620), the Kings Cave deposits may be "several thousand years older" than those at Castle Rocks because the bones were "in a sediment layer that was continuous beneath a rockfall, on top of which there was speleothem development". Even so, they are unlikely to be older than Holocene.

A long series of dates from deposits in various sites in the Oparara caves confirmed the presence of Haast's Eagle in the area from 20 600±450 to 10 880±100 years BP (Millener 1984; Worthy 1987; Worthy & Mildenhall 1989). Most of the eagle material was dated by presence in layers whose upper and lower limits had been established by dates on moa bone collagen.

Where direct dating was unavailable, as in most dune sites, or the association between dated layers and fossil material was tenuous, different

Table 8.3 Radiocarbon dates (^{14}C years BP) for natural and man-associated eagle sites and localities. Gizzard refers to remains of gizzard contents recovered with a skeleton of that taxon. Note that several of the dates published in McCulloch & Trotter (1979) had been published previously. Site name for dates for Graveyard, Eagle Roost, and His Cave material include the fossil site numbers, which all refer to NZMS 260 Sheet L27 (e.g., L27/f100). Continued on next page. See also Notes and References on next page.

Locality/site	FR no.	INS no.	Material	Date	SE	Ref.
Albury Park		NZ1726	Pachyornis femur	7390	160	1
AR 144		NZA360	Hemiphaga novaeseelandiae	10950	110	6
Cannibal Bay		NZ147		390	39	2
Cape Wanbrow 4.1 m		NZ147	Emeus and Euryapteryx	20300	600	3
5.0 m		NZ3093	Emeus and Euryapteryx	32500	2500	3
South		NZA753	Wood charcoal	26500	1400	2
Old Rifle Butts	136/f1212			35900	1700	4
Eagle Roost	L27/f91	NZ6526	Dinornis torosus	11440	140	7
	L27/f93	NZ6526	Dinornis torosus	11800	200	5
	L27/f93		Megalapteryx didinus	11250	150	5
	L27/f93	NZ6569	Megalapteryx didinus	10880	100	7
		NZA358	Coenocorypha	15320	240	6
		NZA359	Callaeas cinerea	10300	280	6
		NZA361	Harpagornis moorei S22472.13	15530	200	6
Enfield		NZ1727	Euryapteryx geranoides collagen	2020	70	1
Glenmark Haast coll.		NZ1729	Pachyornis elephantopus collagen	2730	70	1
		NZA943	moa bone	7110	109	2
Graveyard L2	L27/f100	NZ7317	Megalapteryx didinus	11200	150	5
L3	L27/f88	NZ6453	Pachyornis australis	15680	210	7
top L3	L27/f88	NZ6453	Pachyornis australis	16200	300	5
base S1 L3	L27/f101	NZ7316	Megalapteryx didinus	19300	400	5
base S2 L3	L27/f103	NZ7292	Pachyornis australis	20600	450	5
base S2 L3	L27/f109	NZ7323	Pachyornis australis	18600	230	5
Lag	L27/f90	NZ6586	Pachyornis elephantopus	14030	140	7
Lag	L27/f90		Pachyornis elephantopus	14500	250	5
S1 Lag	L27/f102	NZ7319	Megalapteryx didinus	10980	140	5

Table 8.3 continued Radiocarbon dates (years BP) for natural and man-associated eagle sites and localities. Gizzard refers to remains of gizzard contents recovered with a skeleton of that taxon. Note that several of the dates published in McCulloch & Trotter (1979) had been published previously. Site name for dates for Graveyard, Eagle Roost, and His Cave material include the fossil site numbers, which all refer to NZMS 260 Sheet L27 (e.g., L27/f100).

Locality/site	FR no.	INS no.	Material	Date	SE	Ref.
His Cave	L27/f108	NZ7321	Dinornis novaezealandiae femur	7390	240	8
Mount Owen	NZA605	NZA605	Harpagornis moorei fibula	10950	110	9
Pyramid Valley		NZ610	Emeus crassus bone	3600	45	1
68-73 cm		NZ619	Seeds and twigs	2620	49	2
81-86 cm		NZ620	Seeds and twigs	2930	63	2
		NZ623	Euryapteryx geranoides gizzard	3450	71	1
		NZ624	Dinornis giganteus gizzard	3640	72	1
		NZ625	Emeus crassus gizzard	3740	72	1
		NZ3936	Dinornis giganteus vertebra	3480	80	1
		NZ3590	Dinornis giganteus gizzard	3590	60	1
Waingongoro river mouth		NZ717		552	45	2
		NZ718		699	61	2
oven		NZ543		1018	49	2
		NZ544		752	60	2
Wairau Bar upper layer		NZ50		909	48	2
Wairau Bar		NZ1837	Aragonite	683	41	2
		NZ1838	Euryapteryx	587	58	2
		NZ6480		14190	180	10
		NZ6589		14060	180	10

References: 1, McCulloch & Trotter (1979); 2, Anderson (1990) [Anderson (1990) is based on the Jansen list of Institute of Nuclear Sciences dates from 1955 to 1985, which may be further revised (Anderson 1990)]; 3, Burrows, in (3); 4, Grant-Mackie & Scarlett (1973); 5, Worthy & Mildenhall (1989) NT½; 6, THW pers comm; 7, R Sparks via THW pers comm; 8, Worthy (1987); 9, P R Millener pers comm; 10, R Sparks pers comm.

Note 1: Dates NZ3092 and NZ3093 for Cape Wanbrow have been recalculated as >17300 and >26100 BP, respectively. Both samples had very low collagen levels. (W H Melhuish, pers. comm. to T H Worthy, 27 Feb 1989).

Note 2: "Eagle Roost All material lay in 1-10 cm thick deposit on top of stream-laid gravels; however, the biggest cobbles protruded through more recent faunal deposits. NZA358 Material, selected from the back of the deposit against the wall and deep down the crack, was thought to be as old as any material present from the stratigraphy. The eagle material associated with NZA361 was well scattered. I believe that the eagles probably died in the more exposed area of the site and that their bones moved down slope in several directions. Since then, the rock fall in in the middle of the site has been to a large part destroyed by drip erosion. Individual eagle bones were up to 10 m distant from other parts of the same individual. NZA359 This was a random bone off the surface. The presence of starling and rat bones in the deposit as well is evidence for deposition continuing to the present day." (T H Worthy, pers. comm. in litt.)

Note 3: Unnumbered date for Old Rifle Butts is >35900 years BP.

criteria were used to put upper and lower bounds on the age of a deposit. The basis of dune dating was the assumption that the major coastal dune systems were formed when the sea level stabilised after the post-glacial rise that peaked about 6 000-7 000 years BP (Pickrill 1976, quoted by Brown 1983).

Bone deposited in major coastal dune sites was assumed therefore to be <7 000 years old. Major bone deposits in dunes at Tokerau Bay in Northland were in palaeosols between 1 130±70 and 4 290±100 years old (Millener 1981), a time when the typical vegetation of the area was light forest and shrubland (Dodson *et al.* 1988).

Dates from archaeological sites that may or may not have been associated with eagle remains in the same deposits were as young as 390±39 years BP (Cannibal Bay). If the artefacts found at Wairau and Sumner indicate contemporaneity between cultural layers and eagles, the latest survival of eagles would be between 909±48 and 587±58 years BP.

Stratigraphic evidence suggested that some sites were much older. ^{14}C dates for the fossiliferous beds at Cape Wanbrow of up to 32 500±2500 (Burrows, in McCulloch & Trotter 1979) and >35 900±1 700 years BP (Old Rifle Butts, (fossil site ref. S136/f1212, Grant-Mackie & Scarlett 1973) are towards the upper limit of conventional carbon dating, and the deposits may be older. The thick layers of loess overlying the fossiliferous lenses at Old Rifle Butts suggest a last interglacial age (Grant-Mackie & Scarlett 1973), perhaps as old as c 80 000 years.

The Glenmark Creek sites described briefly by Haast (1872, 1874, 1879) and the Motunau site investigated and described by McKay (1882) were of special interest because their stratigraphy not only suggests at least a last interglacial age, but that similar conditions existed before and after a long break. The covering gravels and silt layers at both localities were deep, and the bones were often crushed and in poor condition (Haast 1879; McKay 1882). Evidence exists for at least two forests at the Motunau site after the fossiliferous peat had been deposited. Periods of deposition and erosion separated the first forest (represented by stumps in growth position), and the forest recently cleared from the coastal plain, represented today by scrub remnants in the adjacent hills.

At Glenmark, the deeply buried deposits of Glenmark Creek 1 and 2 contained eagle, moa, and other bird remains in sediments that had been eroded before, and lay unconformably under the lake swamp in which the type material was deposited. The stratigraphic separation implies a large time gap between the two deposits, for which there is no local record.

A similar gap, with recurrence of similar faunas after a long apparent absence, was apparent near Oamaru. There, however, the sites were further apart than the ones at Glenmark. The Holocene sites at Kapua, Enfield, and Ngapara are within a few kilometres of the much older Cape Wanbrow sites.

At Oparara, the dated sequences provided evidence for changes in geographical distribution of eagles and other taxa across the Pleistocene-Holocene boundary. The changes were apparently synchronous with changes in the local vegetation. Eagle bones were not found in strata deposited later than about 10 500 years BP (Worthy 1987; Worthy & Mildenhall 1989).

8.5 FOSSIL SAMPLE ANALYSIS

8.5.1 General

After January 1990, two almost complete associated specimens became available. Using these, and partial skeletons of three others, it was possible to estimate the variation in bone length proportions within and between limbs and the major axial elements. As a result, estimates of minimum numbers of individuals (MNI) from each site could be based on comparisons of bone lengths as well as on the number of the best represented element. I have followed the operational interpretation used by Van Valen & Sloan (1965), who separated specimens by size before counting MNI. This computational approach differs from that used by Shotwell (1958), who coined the term MNI for the concept introduced by Stock (1929) and Howard (1930), and involved only the number of the best-represented element in the sample.

Interlimb proportions of known single specimens enabled separation of site complexes into specimens. Dimensions were useful at most sites, but could not be used effectively for material that had been retrieved from various unknown

locations within a large site, or where very similar-sized individuals had been preserved together. At most sites, and for elements such as the pedal phalanges, where intermembral ratios were less certain, some ambiguity remained.

8.5.2 Methods

Elements/specimens Elements were assigned to specimens in two stages. First, an MNI was estimated from the number of ipsilateral elements of the best represented bone (Leach 1979). Any contralateral examples of that element were then matched to examples in the series by comparing bone length. Percentage differences between lengths of contralateral main limb elements varied from <0.10% to nearly 0.7% (Table 8.4). Bones were accepted as being from the same individual if the difference in their lengths was less than ±0.7% of bone length (twice the standard deviation for a range of length differences for bones from the known individuals, Table 8.4). If this criterion was not fulfilled for any element, it was taken to be from another individual. The MNI was increased by the number of unmatched elements.

Other limb and axial elements were tested against the master series and each other, using intermembral element length ratios derived from the known individuals (Table 8.5). Using these ratios, even single bones in the sample could be accepted or rejected as representing another individual, so long as their length could be measured accurately. The procedure, as applied to the major limb elements from Enfield, is illustrated in Table 8.6.

8.5.3 The bone sample

At least 655 separate elements in collections could be firmly attributed to *Harpagornis moorei*. Representation of the various elements in the total sample is shown in Fig. 8.45, where the individual elements of the hyoid apparatus, pedal, and pedal ungual phalanges were treated as groups, without differentiation between proximal or distal parts, or digits, respectively. Contralateral elements were grouped. The histogram shows that major bones of the pectoral and pelvic girdles and limbs were most abundant in the sample. Smaller, more delicate elements, such as small bones of the palate and skull, and

Table 8.4 Percentage difference between lengths (in mm) of same element from each side of known individuals.

Element	Number	Length (mm)		Difference
		Side 1	Side 2	Δ%
Scapula	C 40.8	118.9	118.1	-0.67
Humerus	S 27773	233.6	234.0	0.17
	C 40.8	214.5	214.2	-0.14
Ulna	C 40.8	230.4	227.2+	
Radius	C 40.8	211.7	212.5	0.38
Femur	S 27773	170.4	171.0	0.35
	C 40.8	151.1	150.5	-0.40
Tibiotarsus	C 40.8	221.1	221.3	0.09
Tarsometatarsus	S 27773	154.5	154.0	-0.32
	C 40.8	141.4	141.8	0.28
Mean				0.31±0.058%

95% CI = Mean ± 2.SD
= 0.31 ± 2.0.174
= 0.31 ± 0.348
≈ 0.31 ± 0.35%

Therefore, if the unabraded length of a bone was within ±0.35% of the length of a contralateral element from the same site, then the second bone was assumed to be from the same specimen as the first, unless other factors made such a match impossible or unlikely (such as the presence of another element within the same limits, as at Enfield).

Table 8.5 Dimensions and proportions of bones of axial elements and within and between limbs, for left elements of known specimens. Dimensions in mm. Mean equals ratio of mean lengths for whole sample. Cra, cranium; Man, mandible; Ste, sternum; Cor, coracoid; Sca, scapula; Hum, humerus; Uln, ulna; Rad, radius; Cpm, carpometacarpus; Pel, pelvis; Pyg, pygostyle; Fem, femur; Tbt, tibiotarsus; Tmt, tarsometatarsus. H, estimate based on humerus length ratio; T, estimate based on tibiotarsus ratio. Values in parentheses are based on element lengths derived from length ratios.

		Specimen						
Element	Ratio	OMNZ C 40.8		NMNZ S 27773		NMNZ DM 2134		Mean
Cranium		151.2		164.3		165.5*		
Mandible	Man/Cra	116.7	0.77	124.2	0.76	126.5	0.76	0.76
Sternum	Ste/Hum	140.3	0.65	155.1+	0.66	163.0	0.68	0.66
	Fem/Ste		0.93		0.91		(0.93)	
Coracoid	Cor/Hum	89.1	0.42	97.5	0.42	106.0	0.44	0.40
	Cor/Cra		0.59		0.59		0.64	
	Cor/Cpm		0.82		0.78		0.85	0.50
	Cor/Tmt		0.63		0.63		0.66	
Scapula	Sca/Hum	118.9	0.55	127.0	0.54	133.0	0.55	0.55
Humerus	Hum/Cra	214.5	1.42	233.6	1.42	241.0*	1.46	1.46
	Hum/Tmt		1.49		1.52		1.51	
Ulna	Uln/Hum	230.4	1.07	252.5	1.08	258.4+	1.07	1.09
Radius	Rad/Hum	211.7	0.99	237.2	1.02	245.4	1.02	1.01
	Rad/Uln		0.92		0.94		0.95	
Carpomet	Cpm/Hum	108.4(R)	0.51	124.9	0.53	125.4	0.52	0.50
	Cpm/Fem		0.72		0.73			
Pelvis	Pel/Hum	165.5	0.77	182±	0.78	197.5	0.82	0.75
	Pel/Fem		1.10		1.07		(1.12)	
Pygostyle	Pyg/Fem			54.0	0.32	56.0	0.34	
Femur	Fem/Hum	151.1	0.70	170.4	0.73	175.5H	174.1T	0.70
	Fem/Cra		1.00		1.04			1.00
Tibiotarsus	Tbt/Fem	221.1	1.46	241.1	1.41	247.2	(1.41)	1.45
Tarsometat	Tmt/Fem	141.4	0.94	154.5	0.91	160.8	0.92H	0.91
	Tmt/Tbt		0.64		0.64		0.65	0.63
	Tmt/Hum		0.66		0.66		0.67	0.66

Table 8.6 Dimensions of contralateral bones from Enfield, illustrating the calculation of MNI from side representation and length of elements.

	Side			
	Left		Right	
Element	Number	Length	Length	Number
Humerus	BMNH 8	228.2	-	
		-	232.9	BMNH 9
	A 423 BMNH	233.3	-	
Ulna	BMNH 12	241.4	-	
	AV 5329	247.8	-	
		-	248.8	BMNH 13
Radius	A 423 BMNH	223.8*	-	
	BMNH 14	232.2	232.9	BMNH none
		-	233.6	AV 5329
Carpometacarpus		-	-	
	R 3184 BMNH	117.8	-	
	BMNH 35	118.9	-	
			120.4	BMNH 36
Femur		-	-	
	BMNH 10	163.6	-	
		-	163.1+	BMNH 11
Tibiotarsus		-	-	
	BMNH 16	236.8	-	
		-	239.6	BMNH 15
Tarsometatarsus		-	-	
		-	152.6	AV 5329
	BMNH 19	153.2	153.4	BMNH 16

*, radius somewhat shorter than would be expexted for specimen represented by humerus BMNH 8 and may represent a fourth bird. The BMNH numbers given as simple digits should probably be prefaced by 93.1.30. (marked on cranium with same collection data; sequence refers to 30th specimen catalogued in January 1893). Femur BMNH 11 entered representing different specimen than BMNH 10 femur because element widths differ markedly.

The possible fourth bird represented by a carpometacarpus was not included in the MNI for Enfield because there is greater variation in the lengths of contralateral bones for this element than any other, based on the dimensions of the smaller Castle Rocks individual. The matching of the Enfield carpometacarpi is too close to allow the presence of another bird on this element alone. An alternative explanation that the disparity evident in the Castle Rocks individual was because of mixing with a third individual was not supported by the consistency of size range wothin the samples attributed to the two recognised specimens.

phalanges of the manus were least common, and major axial elements such as cranium, sternum, and pelvis were intermediate in frequency. Although the proportion varied markedly between elements, no significant difference ($P >> 0.05$; Student's $t = 0.2133$, 50 df) was found between the means of 26 left and right side elements (excluding ribs and pedal phalanges). The total number of identified left elements was 197, as against 187 right side elements.

Some of the more fragile elements were found only under exceptional conditions of preservation. Examples are the hyoid apparatus and posteropterygoid from AR 144. However, excavation technique and knowledge on the part of the excavator of the possibility of finding smaller material also affected the representation of some elements in the sample. Quadrates, for example, are reasonably robust bones, but have been recovered from only those sites where special care was taken to locate all smaller bones (Castle Rock, Pyramid Valley, and Mount Owen).

Some of the larger bones were identified from fragments, and could be grouped with intact elements. Thus, several 'crania' were represented by the tip of the premaxilla. A premaxilla tip qualified as an element according to the criterion of Holtzman (1979).

Several smaller elements were represented only in the collection from Mount Owen, where a unique combination of favourable factors existed. The specimen was relatively young (c 2 160 years). The site was almost inaccessible. One scavenger (a weka *Gallirallus australis*) is known to have entered it after the eagle. Because the site was on a ridge, there was little water flow through it part from meltwater draining into the chamber under the shaft. The specimen lay on a pile of cobbles that provided drainage and protection for smaller elements which dropped away from the carcase as it rotted (Fig. 8.18F). Human disturbance was minimal because the first visitor to the cave knew enough about fossil bird bones to respect the material and to report it to a competent person. Finally, the collection team was aware that a complete skeleton might be present and used a checklist to guide the search under difficult collection conditions.

The proportion of vertebrae, pedal phalanges, and ribs in the total sample was biased by the full and almost full complements for individuals from Mount

Owen and Castle Rocks. The bias is illustrated by a comparison of Fig. 8.45 with Fig. 8.46, in which these elements of the Mount Owen specimen have been omitted.

The probability that an eagle bone taken at random from the sample is a particular bone of the skeleton (Fig. 8.47) also illustrates the bias introduced to the sample by almost complete specimens. This probability was calculated as the proportion of each bone type in the sample, divided by the number of that element in a skeleton (without differentiating between the different vertebrae or pedal phalanges). They are estimates of the conditional probability that, given the presence of eagle bones in a deposit, the bones will be particular elements. Larger, more durable and conspicuous elements had probabilities ≥ 0.04, the tarsometatarsus and tibiotarsus ≥ 0.07, and all but one of the more fragile, or more easily overlooked, elements (e.g., posteropterygoid, hyoid, scleral ossicles, metatarsal, and alar phalanges) had probabilities ≤ 0.02, with most < 0.01.

The *a posteriori* probability of particular bones occurring in the sample, compared with their probability of being drawn at random from an individual, is shown in Fig. 8.48. These probabilities emphasised the disproportionately high loss rates of smaller elements between death of the individual and sampling.

The survival of bones in a deposit, between deposition and excavation, is a complex function of the processes of fragmentation, deposition, diagenetic processes during burial or surface preservation, and exposure. Their representation in a sample involves factors such as the observational abilities of collectors, and the techniques employed in excavation.

An index of survivability for each element in the skeleton was derived from the sample (Fig. 8.49). Higher values indicate longer persistence coupled with sufficient conspicuity to attract human attention. The survival index was calculated as the probability of an eagle bone being a particular element compared with the probability of a bone drawn from a single skeleton being a particular element (i.e. the quotient of the sample and individual probabilities).

The principal advantage of this index over the individual probabilities, is that it combines the sample and individual values in one measure, and has a greater numerical range, with values typically being between zero and five, as

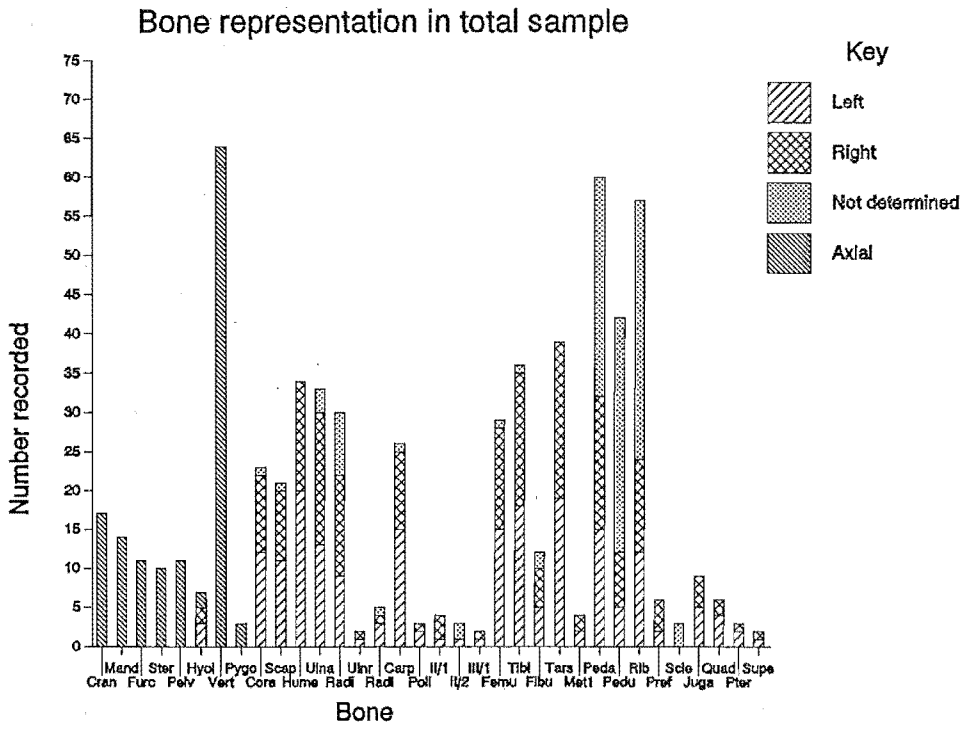

Fig. 8.45 Representation of elements of Haast's Eagle in total sample (all sites with known material). Note numbers of small elements, cf. Fig. 8.46.

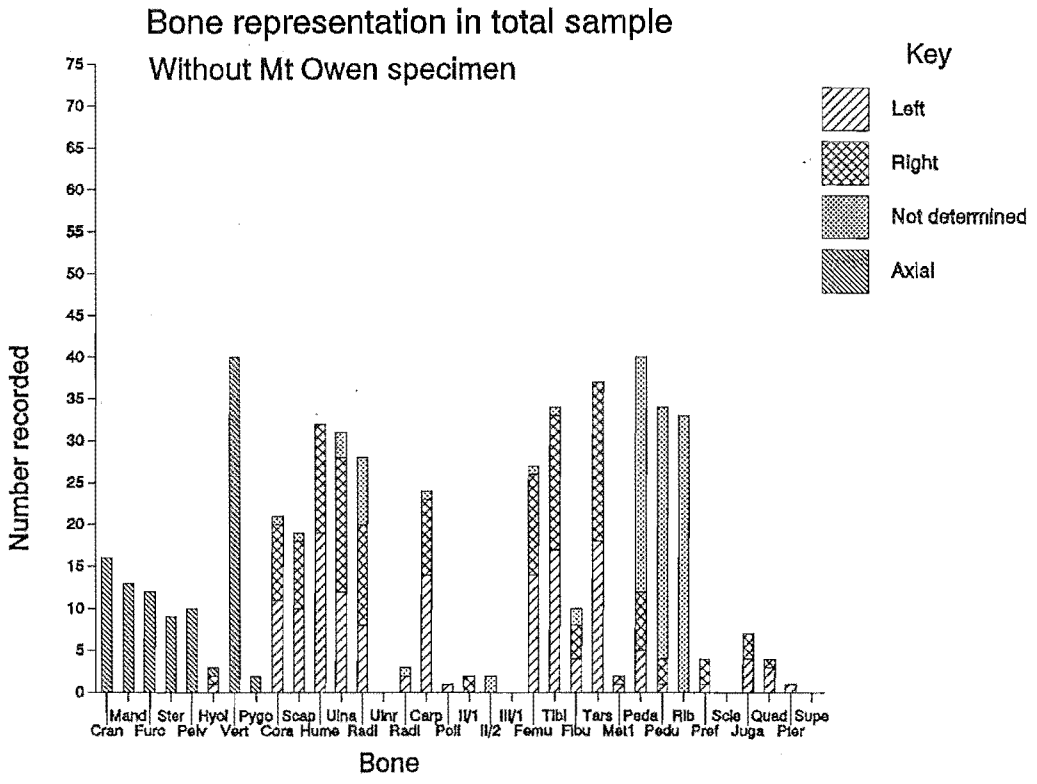

Fig. 8.46 Representation of elements of Haast's Eagle in total sample, excluding the specimen from Mount Owen (S 27773). Note lower numbers of small elements than in Fig. 8.45.

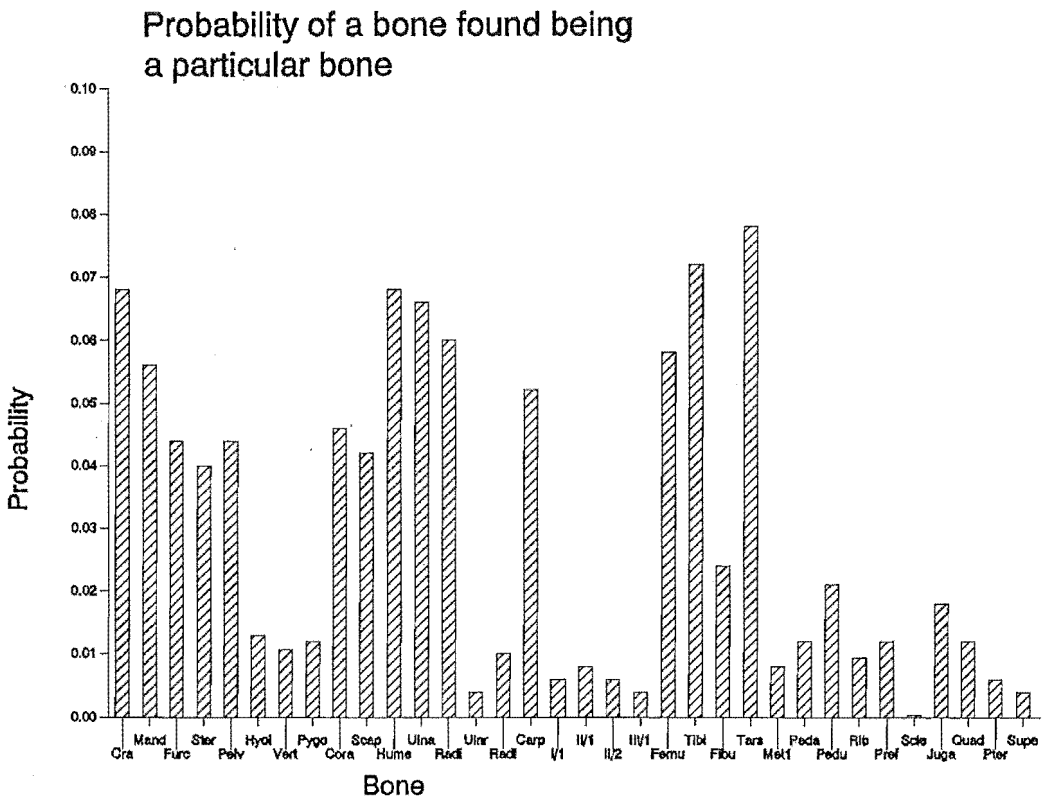

Fig. 8.47 *A posteriori* probabilities that the next eagle bone found in the total sample will be a particular element.

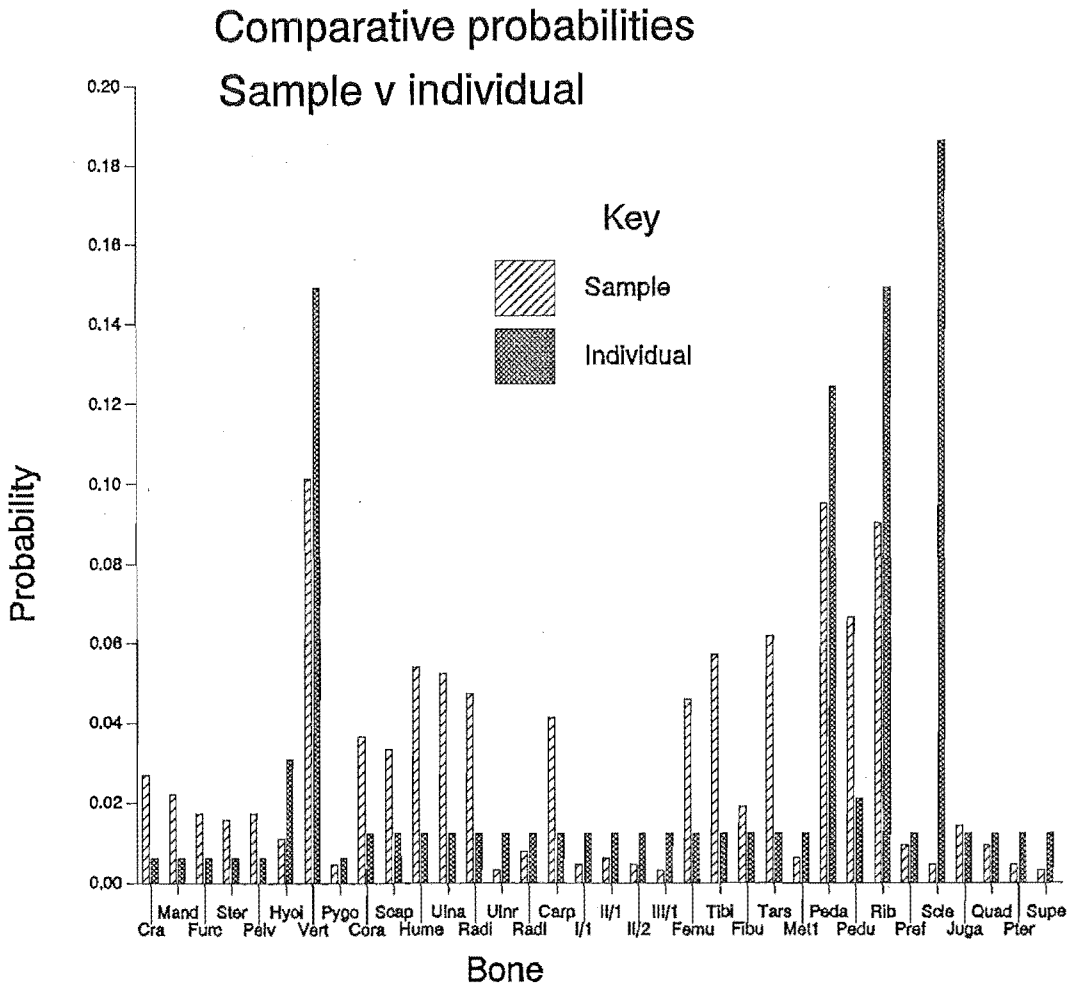

Fig. 8.48 *A posteriori* probabilities that the next bone of an individual eagle will be a particular element: hatched, in sample; solid, known individual.

such it provides greater perception of the differences involved. The histogram obtained (Fig. 8.49) is substantially the same shape as that in Fig. 8.47, but the differences between the elements are accentuated, especially for the pedal ungual phalanges.

The minimum number of individuals represented by each element is summarised in Fig. 8.50. This MNI was the sum of all individuals represented by that element over all sites, taking into account deviations in contralateral dimensions and intermembral proportions of known individuals (Table 8.4). The general pattern observed in the previous histograms was repeated: more specimens were represented by large than by small elements. However, some differences were apparent. More individuals were represented by humeri and tibiotarsi than by tarsometatarsi, and fewer by axial elements than expected from patterns of bone survivability. This trend is not only the result of there being, for example, only one cranium per animal against two of each of the limb bones, but also because of the increased likelihood of single bones in exposed sites, such as dunes, being one of the more robust limb bones.

Nineteen individuals in the sample were represented by single elements (Fig. 8.51), and thirteen were from sites containing only a single bone. The other six could not be assigned to other individuals known from their respective sites. The distribution was skewed strongly to the right, and bimodal. This probably resulted from interaction between the chances of material being preserved at a site, and its being found. In dunes and rock shelters, material tends to be exposed piecemeal, and single elements removed from the main deposit by wind or other agents may be collected by casual observers.

In contrast, caves or swamps are usually explored deliberately, and several elements are collected. Many more individuals were represented by one or a few elements because the exceptional circumstances necessary for preservation of many smaller elements are rare.

The number of individuals for which bones were identified by size is shown in Fig. 8.51 (open bars). The distribution was both lower, and more skewed to the right in the mid-range, when the residue of unmeasurable elements from each site were assigned to individuals on the basis of proportions

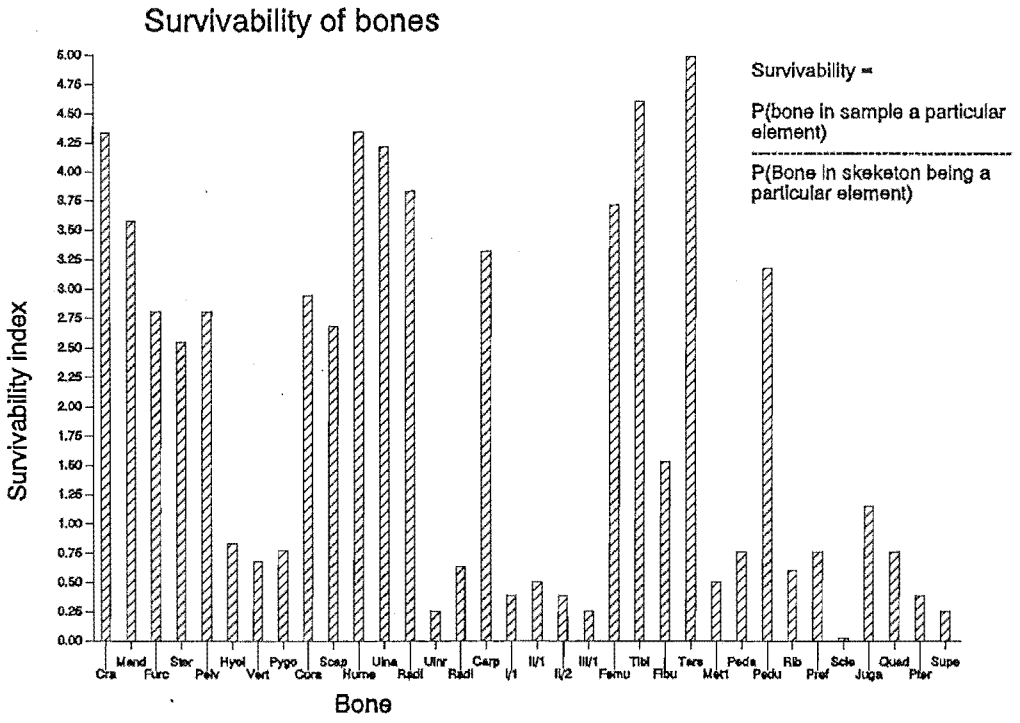

Fig. 8.49 Index of survivability for different elements in the skeleton, from proportional representation in fossil sample of Haast's Eagle.

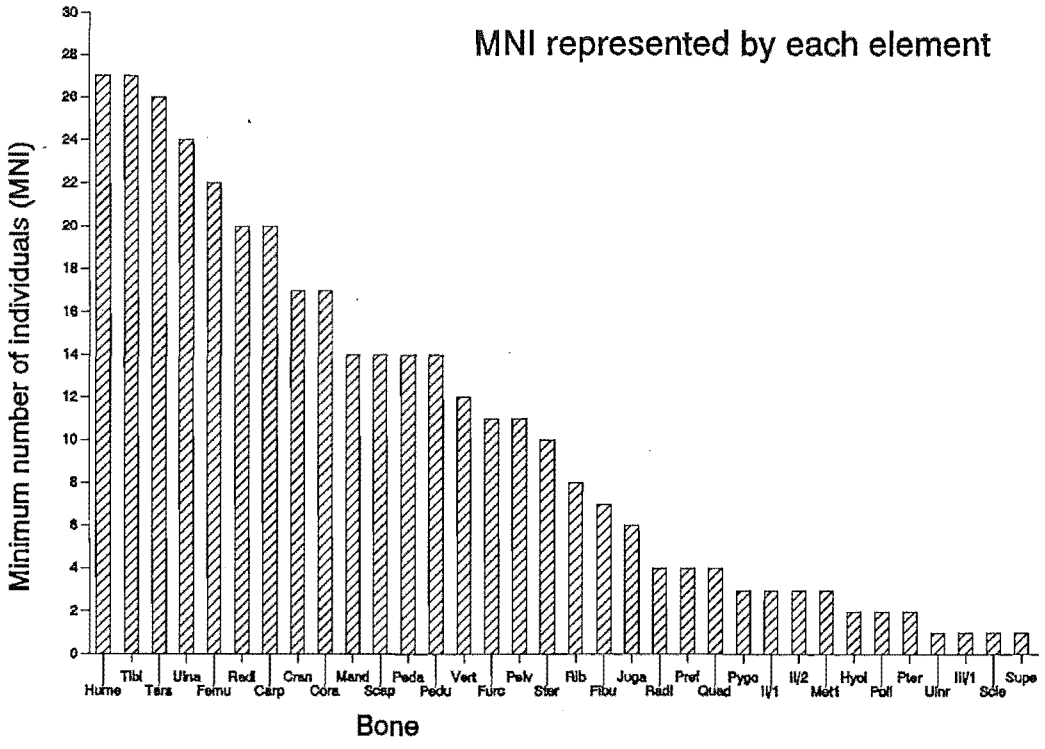

Fig. 8.50 Minimum number of individual eagles represented by each element, in descending order of representation along x axis.

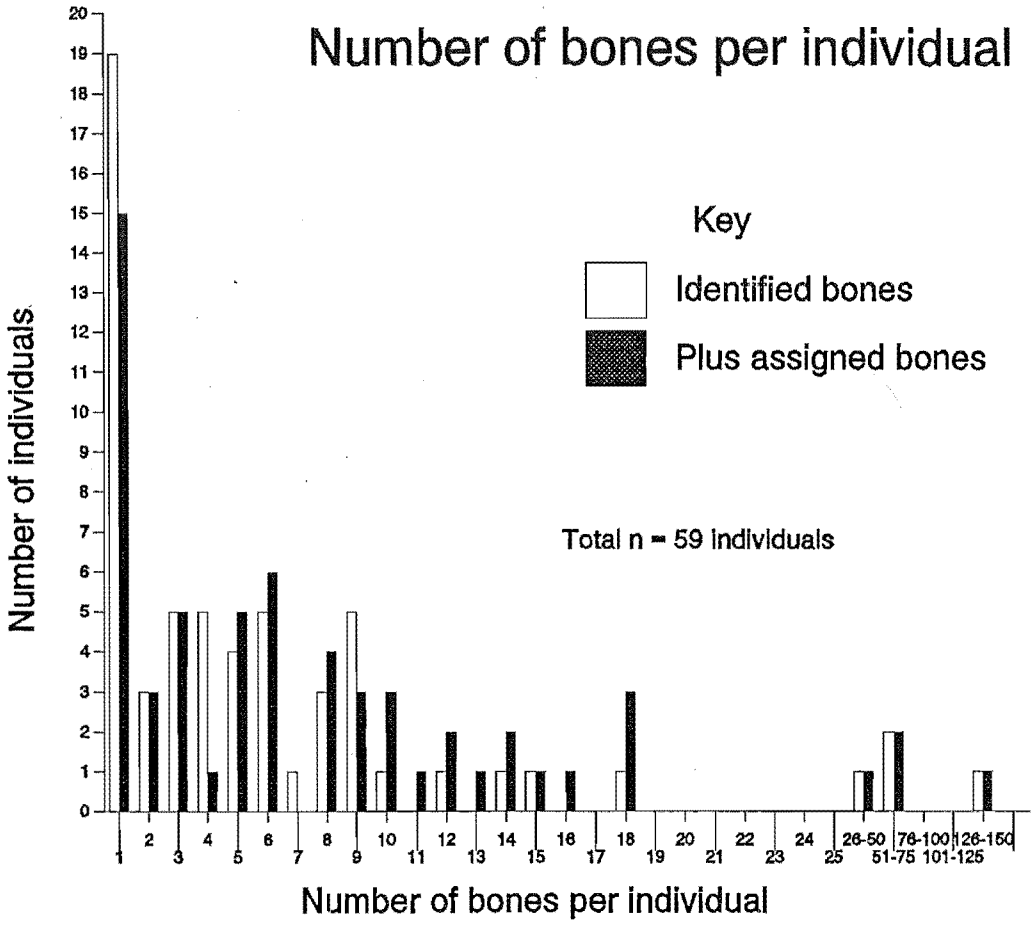

Fig. 8.51 Number of individual Haast's Eagles represented by different individual sample sizes. open bars, based on bones identified to individuals; filled bars, identified bones plus those assigned by proportion of total sample.

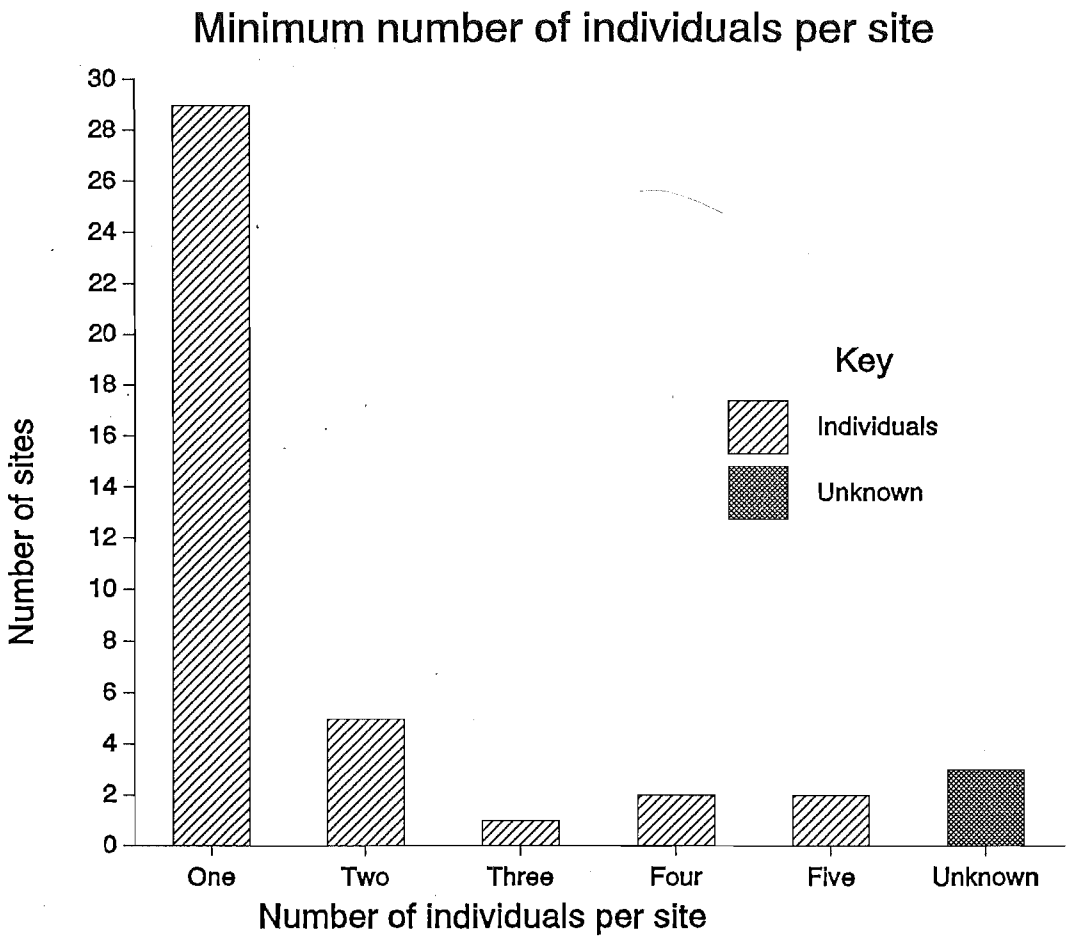

Fig. 8.52 Number of sites containing different numbers of identified individual eagles.

Table 8.7 Number of elements, minimum number of individuals (MNI), number of elements per individual in order of identification, and number of unassigned elements for each site. No., number of elements; MNI, minimum number of individuals from side counts and dimensional analysis; NA, elements not assigned to an individual; MA, Mean number of elements from that site assigned to individuals; OM, overall mean of elements from that site per identified individuals.

Site	No.	MNI	No. of elements per individual for individual number					Elements/individual/site		
			1	2	3	4	5	NA	MA	OM
Albury Park	3	1	3						3.0	3.0
AR 144	18	1	18						18.0	18.0
Cannibal Bay	1	1	1						1.0	1.0
Castle Rocks	125	2	53	72					62.5	62.5
Dunstan Range	1	1	1						1.0	1.0
E entrance	1	1	1						1.0	1.0
Eagle Roost	39	2	7	27				5	17.0	19.5
Enfield	33	3	4	9	8			12	7.0	11.0
Glenmark Creek	1	1	1						1.0	1.0
Glenmark/East	12	1	12						12.0	12.0
Glenmark/West	15	1	15						15.0	15.0
Glenmark Creek 2	1	1	1						1.0	1.0
Golden Point	?	?	?							
Graveyard	48	5	6	6	5	4	2	25	4.6	9.6
Hamilton Swamp	13	2	5	1				7	3.0	6.5
Hamilton Gully	1	1	1						1.0	1.0
His Cave	59	5	9	9	3	3	6	29	6.0	11.8
Hives extension	4	1	4						4.0	4.0
Holyoake Stream	1*	1	1*						1.0	1.0
Hunterville	?	?	?							
Kakanui Beach	2	1	2						2.0	2.0
Kapua	1	1	1						1.0	1.0
Kings Cave	3	1	3						3.0	3.0
Marfells Beach	17	4	3	1	1	1		11	1.5	4.25
Motunau	15	2	4	2				9	3.0	7.5
Mount Owen	127	1	127						127.0	127.0
Ngapara	19	2	9	6				4	7.5	9.5
Oaro	5	1	5						5.0	5.0
Obelisk Range	1	1	1						1.0	1.0
Old Rifle Butts	14	1	14						14.0	14.0

Table 8.7 continued Number of elements, minimum number of individuals (MNI), number of elements per individual in order of identification, and number of unassigned elements for each site. No., number of elements; MNI, minimum number of individuals from side counts and dimensional analysis; NA, elements not assigned to an individual; MA, Mean number of elements from that site assigned to individuals; OM, overall mean of elements from that site per identified individuals.

			No. of elements per individual for individual number					Elements/individual/site		
Site	No.	MNI	1	2	3	4	5	NA	MA	OM
Orepuki	6	1	6						6.0	6.0
Puketapu	?	?	?							
Pyramid Valley	17	4	4	8	1	1		3	3.5	4.25
Sumner	1	1	1						1.0	1.0
Te Aute no. 2	9	1	9						9.0	9.0
Waingongoro	1	1	1						1.0	1.0
Waipapa Point	1	1	1						1.0	1.0
Wairau Bar	5	1	5					2	3.0	5.0
Wakapatu	8	1	8					3	8.0	8.0
Wanbrow	10	1	10						10.0	10.0
Warrington	1	1	1						1.0	1.0
No locality	16							16		
Sample size	655	59+3	356	141	18	9	8	123		
No. of sites	38	38	38	10	5	4	2	11	38	38
Mean (655)	17.24	1.55	9.42	14.1	3.6	2.25	4.0	11.18	9.67	10.54

of identified elements (Fig. 8.51, solid bars). Material was assigned on the assumption that the best-represented individuals should, on average, be best represented amongst the unknown material, at best a crude criterion. It may be argued that the least represented individual from identified material was more likely to be represented amongst the fragments. However, other factors such as time available for attrition within the deposit were unknown, and these would have reduced the number of elements from individuals which had been in the deposit for a longer period. Other factors, such as different diagenetic and erosive processes, could also bias the data the other way. On average, the distribution shown by solid bars in Fig. 8.51 probably approximates the probability distribution for the representation of an individual in a sample from a site. As such, the number of bones per individual at a site can be viewed as a measure of site quality.

Number of sites and number of individuals per site were inversely related (Fig. 8.52). Twenty-nine sites (74%) contained a single identified individual, represented by one or more elements, and 10 (26%) had more than one individual. Eight of 29 sites (28%) contained only one bone (Table 8.7). It would be almost impossible to prove that individuals were trapped at the same time, even if all individuals from a site were radiometrically dated. However, larger and smaller birds in each of the six instances where two were in the same deposit suggests that pairs were involved.

The minimum number of individuals known from each site and the number of elements are summarised in Table 8.7. At least 60 individuals were identified, not including those from sites from which material has not been located in collections (Hunterville, Puketapu, and Golden Point) At any one site, the material ranged from a single element, to substantially complete skeletons (Table 8.7), and the minimum number of individuals (MNI), from one to five (Table 8.7; Fig. 8.52).

8.6 TAPHONOMY

8.6.1 Dismemberment and scattering

The process of disarticulation varied with the type of deposit. In swamps, carcases were probably deposited in anaerobic sediments soon after the flesh had decayed. Burrows (1989) suggested that eels and other fish may have contributed to the disarticulation and scattering of skeletons in Pyramid Valley.

The quality of preservation varied with the kind of sediment. In peat, bones were often stained dark brown or black (as at Kapua or Enfield, Fig. 6.4), but where they were protected the preservation of detail was excellent.

Bones from springhole swamps were often broken or abraded, especially if they had been mixed with quantities of moa bones, as at Enfield or Hamilton. Material recovered from the Motunau peat layer consisted only of those elements that had survived crushing, and the cranium had been protected by a large moa bone (McKay 1882). According to McKay (1882), many of the bones in the peat were soft and present in outline only.

The Albury Park springhole was unusual in that the source was suspected to be a pothole in the limestone on the ridge above (Mrs B. McCulloch, pers. comm. 1990). From there, the bones were apparently carried by water through fissures into the swamp where they were preserved in peat.

Birds that died in caves usually decayed *in situ*, and the only disturbance was apparently from trampling by other birds before they too died. The best example of *in situ* decay and disarticulation with limited scattering was the specimen in SO 209 on Mount Owen (Fig. 8.18). When discovered, most of the bones remained where they had fallen during decay, after the body had distorted *post mortem*. The elements were not articulated, but were arranged in a recognisable pattern (T H Worthy pers. comm.; Fig. 8.18F). The only element transported from the area of the carcase was the pelvis, which had been carried over a rockfall into the adjoining chamber, presumably by a weka whose remains were also found in the cave.

New Zealand lacked mammalian scavengers until the *kiore* (*Rattus exulans*) was introduced by Polynesians, probably about 1 000 BP (Atkinson 1985). Biogenic disturbance of exposed deposits in caves and dunes was limited.

8.7 PALAEOAUTECOLOGY

8.7.1 General

Of the 41 sites that contained eagle bones, eight were in caves, three in fissures, 13 in swamps, four in dunes, one in a rockshelter, one possibly in loess, two in beach or estuarine deposits, and three with possible archaeological associations (Table 8.1 and site data - Section 8.2.2 - above). The remainder included three with no data (Dunstan; Hunterville; Oaro), one possible swamp site (Golden Point), and two possible middens (Orepuki; Wakapatu; Warrington). Dune sites may have contained material from both natural and cultural layers.

The buried bone-bearing peats, such as those at Motunau and Glenmark Creek 1 and 2, have been classified here as swamp deposits because of their similarity in macrofossil content to more recent deposits.

It was possible to predict the type of sediment many bones had been preserved by their colour and state of preservation. Although it was possible in some instances to infer the type of site and hence the probable location for unprovenanced material from these clues, this was not done as a matter of course. One unlabelled element (a humerus in NMNZ) was assigned to a site, because it was identical in length to a humerus listed from that site by Hamilton (1893) but which had not been located.

8.7.2 Entrapment and deposition

Different mechanisms of entrapment, disarticulation, and deposition operated at different types of site. Eagle bones were deposited at a site in one of four principal ways: by the bird's being unable to fly up steeply enough from an enclosed space; by miring; by natural death at the site; and by human predation.

Eagles may have injured themselves in a pit-type trap, but most birds probably died from thirst or starvation. There is no evidence that any specimens of Haast's Eagle were damaged through injury, but lesions may have been obscured by post-mortem damage.

Birds mired in swamps and shallow lakes were trapped by the legs, body, and wings in a sticky substratum and died of starvation or drowning, or waterlogged in open water and drowned. Birds could also have died naturally

and been deposited in pits or mires *post mortem*.

For sites other than pits or mires, the cause of death was usually unknown. Human predation was implied at some sites (e.g., Wairau, Sumner).

8.7.2.1 *Caves and fissures* All the cave and fissure sites seem to have been non-return traps that eagles could enter but not leave. If there were side passages at the bottom, some birds had moved out of the trap area before dying of thirst or starvation. Material in horizontal cave passages away from the bases of open potholes, showed evidence of having been transported by water or gravity. These bones were abraded and worn, and the larger, stronger bones predominated (see site lists, Section 8.2.2). There was no evidence that eagle material ever entered caves other than through vertical or near vertical shaft entrances.

Some eagles may have died above a cave entrance and fallen in, but most are likely to have had been lured into a cave by the prospect of food. However, eagles and vultures are not known to frequent caves or potholes in normal circumstances to search for food (Brown & Amadon 1968), although one small accipitrid, the Bat Hawk (*Machaerhamphus alcinus*) visits cave entrances where it takes live prey (Brown & Amadon 1968). To attract an eagle into an enclosed situation like a pothole, I suspect that the potential prey would have had to be moving around and making a noise, or calling.

All eagle material found in New Zealand caves and fissures has been in sites where suitable prey could have survived arrival at the bottom of the trap and still have been vocal, and in most instances, mobile. In all cave sites where the entrance shaft still exists, it is possible to see the sky from the bottom of the shaft (T H Worthy, pers. comm.).

A pothole (*tomo*) or fissure would have acted as a trap if it was too narrow for an eagle to have spread its wings fully, or if the angle of climb needed by the bird to fly up to the rim from the bottom exceeded the bird's best climb angle. Eagle remains were found in fissures including that at Castle Rocks, where there was insufficient width for the wings to be spread, but where entry could have been gained by volplaning or gliding on half-closed wings (Fig. 8.4D). The extreme example of an eagle having to entered a cave it could not escape from,

was the bird in SO 209 on Mount Owen (see 8.2.2.18). The bird apparently survived a fall of about 15 m down a vertical shaft no more than one metre wide, because it was found in a chamber separated from the bottom of the shaft by a rockfall. Either it had blundered into the entrance during the night or in fog, or, more likely, had broken through a snowcrust while walking about on the narrow ridge.

There were probably lower and upper depth limits for a trap to be effective. If the trap had been too shallow, a moa or other large flightless bird such as the goose *Cnemiornis* or adzebill (*Aptornis*) acting as bait could have walked out, or alternatively, if the had been trapped by injury the eagle could have climbed out after feeding. In a shallow hole, too, the steepness of the walls and its surface texture (e.g., slickenside v stepped) may have been important.

If the walls had been too high (i.e. the hole too deep), a flightless bird would have been either killed by the fall, and not attracted an eagle's attention by moving around or calling, or have been invisible from the surface. With increasing depth, holes would also have become too dark at the bottom for an eagle to have seen any prey and the narrower the shaft, the shallower this critical depth would have been. The maximum penetration of direct sunlight for two angles of elevation of the sun is plotted on Fig. 8.53: objects would be clearly visible up to about twice this depth, depending on the shape of the *tomo* shaft and amount of vegetation around the entrance.

As can be seen from Fig. 8.53, the lower limit for L depended on D, via angle ⌀, the maximum achievable angle of climb. The lower limit for D was taken as the minimum depth required to trap a flightless bird as large or larger than a goose, a depth that varied with the slope of the walls of the cavity. Moa remains have been found in pits as shallow as 1.5 m, and this is taken as the lower limit for D for a pit with walls of greater than 45° wall angle.

The limiting fissure width (W) was estimated to be 3.5 m, based on the bird's probable wing span, and the need for clearance from the walls while in flight. According to Hamilton (1893), the width of the Castle Rocks fissure was 8 feet (2.44 m), narrowing towards the entrance (see 8.2.2.3 and Fig. 8.4D).

Assuming that W was sufficiently large, a combination of effective length

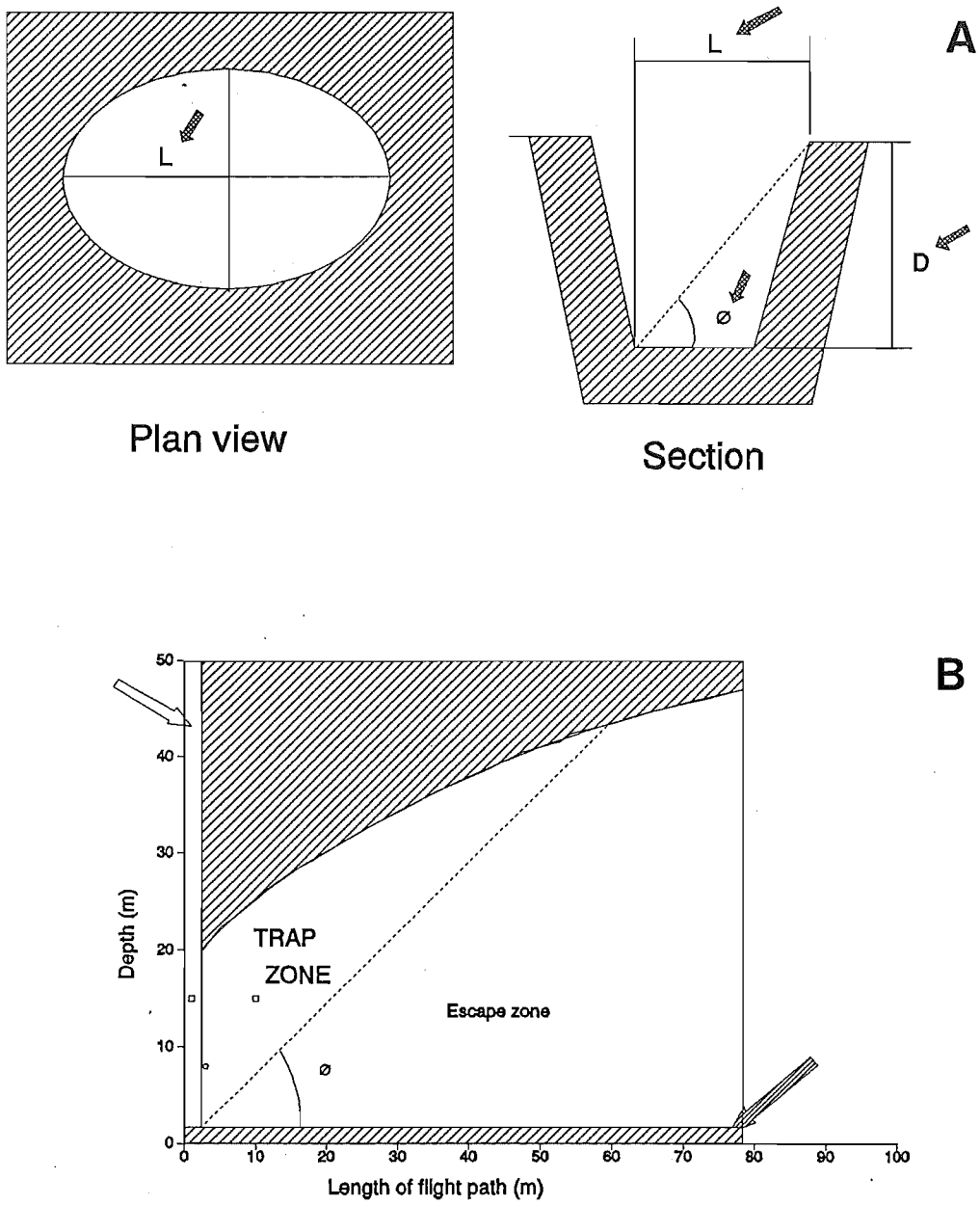

Fig. 8.53 (A, B) Dimensions of pit traps: **A**, schematic plan and section of pit, dimensions arrowed; **B**, depth and flightpath length, upper shading is dark zone. Minimal depth, flight path arrowed.

L and depth D would have defined the climb angle required for an eagle to reach the surface (tan ⌀ = D/L, Fig. 8.53).

There was a greater variety of depositional environments in caves than in other types of site. In some deposits, such as those in AR144, the degree of preservation of eagle bones was remarkable. However, where bones had been transported or lay under dripping ceilings, the bones were often in poor condition. In His Cave, for example, the eagle bones were in a passage several metres downstream from the 10-metre-deep shaft through which the birds had entered. The bones were badly eroded by transport and dripping water (Worthy 1987).

8.7.2.2 *Swamps* The area of most swamp sites during bone deposition is unknown. Springhole swamps may have been only as large as the deposit excavated, judging from the active site at Makirikiri (Worthy 1990). The number of eagles found in these must therefore approach the numbers that actually died and were buried in the swamp.

The area excavated at Pyramid Valley so far, is about 10% of the total area of the swamp deposit. Although the lack of currents implied by the varved sediments and preservation of delicate elements suggest that there was little transport and that any scattering of bones was approximately random, some parts of the swamp are richer in bird bones than others. The richest parts of the deposit are apparently in the lowest section that has already been excavated. Therefore a total of 40 eagles in the whole deposit, assuming that the eagle MNI represents 10% of the total deposited there, is likely to be an upper limit.

Duff (1955) estimated that there were 750-800 moas per acre (c 1 800 ha^{-1}) in the area excavated until then, which gives 2 700 in the 1.5 ha swamp. If so, the maximum estimate would be one eagle for every 67 moa, and the minimum of one per 670 moa.

Because eagle and moa bones have been found in several swamps, it has been assumed that eagles were trapped in swamps and shallow lakes while preying on living or dead moas that had been trapped by soft sediments (Haast 1872; Duff 1949; McCulloch 1991).

However, there is no evidence for such a predation scenario in the site records, nor was any damage consistent with injury during perceived attacks observed on eagle or moa bones. Many moa skeletons from swamps lack crania and cervical vertebrae, and Archey (1941) suggested that Haast's Eagle may have been able to remove these parts selectively from carcases. However, as Eyles (1955) and others have noted, the head and neck would have been the most easily disarticulated parts of the body, and could have drifted away before the rest of the bird was incorporated in the sediments.

[Since the last paragraph was written, clear evidence of direct predation on on moas has been found, in the form of claw puncture marks in pelves from Pyramid Valley and Kapua (Holdaway & Worthy, in prep.). Marks were found on twelve pelves out of 150 examined (T H Worthy, pers. comm.). Most of the individuals were *Emeus crassus*, although most had been identified as *Euryapteryx*. The consistent misidentification of *Emeus* as *Euryapteryx* or *Pachyornis* that was found by Worthy (pers. comm.) during his study of Canterbury Museum collections is potentially a strong source of bias for the results reported in later sections of this work.]

Wild accipitrids are known to be able to survive severe injury to wings (Fox 1977). Several accipitrids, for example sea eagles (*Haliaeetus*), can rise from a water surface, even carrying a load (Brown & Amadon 1968).

Pyramid Valley has amongst the largest recorded fossil avifaunas (Scarlett 1955, 1969), and the highest MNI (4) of Haast's Eagle of any swamp or lake deposit. Birds such as pigeons (*Hemiphaga novaeseelandiae*), kaka (*Nestor meridionalis*), tui (*Prosthemadera novaeseelandiae*), and robins (*Petroica australis*) were preserved in the lake's sediments after apparently dying naturally in its vicinity. It is reasonable to assume that they fell or were washed into the lake as carcases, or were trapped by sticky sediments while drinking at the edge of pools during periods of dry weather. There is no *a priori* reason for invoking any other mechanism for their presence in the sediments, nor indeed for the presence of eagles in this or other swamps. The talons of Haast's Eagle were exceptionally long (see Chapter 2, 2A and 5) and may have been readily caught in soft sediments or tangled vegetation around lake or springhole swamps. Eagle

remains are amongst the most abundant bones at Rancho La Brea in southern California, where asphalt seepages provided a treacherous surface for walking (Howard 1930).

Therefore, although it is possible that eagles were attracted to carrion in the form of dead or dying moas in swamps, and trapped themselves in the process, it cannot be assumed that this was the only, or even one, factor, in the deposition of eagle bones in swamp sediments. Eagle bones in swamps are, in the absence of other information or speculation, evidence only of the presence of eagles near the swamp or lake when bones were being incorporated in its sediments.

The principal difference, therefore, between eagle entrapment in swamps and in caves is that swamps and lakesides are normal habitats for eagles and their prey, whereas caves are not. Living bait was almost certainly *necessary* for eagles to be trapped in most caves, but presence of eagles near a swamp is *sufficient* to explain their presence in swamp deposits.

8.7.2.3 *Dunes* Natural dune occurrences of eagle remains probably represent natural deaths, rather than entrapments. One bird at Marfells Beach was immature (Canterbury Museum catalogue; pers. obs.), but had probably fledged. Mortality is highest amongst fledglings in raptors, as in other birds (Brown & Amadon 1968; van Tyne & Berger 1976).

Most bones from dunes were leached and weathered to a characteristically porous grey (Fig. 6.4). The alar digit from Waingongoro was light and pale (Plate 16), typical of exposed dune material. Elements in dunes were usually scattered. For example, it was impossible to localise the material from Marfells and Grassmere Spit because the site is so large and single elements were found at intervals over many years. One skeleton at Grassmere was substantially intact when found, but the bones were mislaid after collection (J R Eyles pers. comm. August 1990).

Bones usually occurred on older surfaces, including palaeosols exposed by wind blowing away later drifting dunesand.

8.7.2.4 *Humans* The only instances where there was strong circumstantial evidence for predation by humans on Haast's Eagle, were the artefacts fashioned from eagle ulnae and tibiotarsi found at Sumner (8.2.2.27) and Wairau Bar (8.2.2.31). These appear to have been shaped from fresh bone (Falla 1942), and suggest that the birds were at least contemporaneous with Polynesians, if not hunted by them, because abundant swan and other bones would have made searching for fossil bone unnecessary and uneconomic.

The presence of eagle bones in dune systems with extensive early Polynesian midden systems, such as those at Warrington, Orepuki, Cannibal Bay, and Waingongoro, does not in itself prove association between eagles and humans (Millener 1981). Dune systems were forested before humans arrived (Brown 1981; Dodson *et al.* 1988), and even ^{14}C dates on eagle bone from within the Polynesian era would not be conclusive.

8.7.2.5 *Overhangs* The only definite record of Haast's Eagle from a rock overhang was that of a pelvis found near the surface under a schist outcrop on the Obelisk Range near Alexandra in Central Otago. Haast (1874) described the pelvis as having come from a fully grown but young bird, and an examination of the specimen in the BMNH supports this view (pers. obs.). The age of the bird at death, together with the nature of the site, raises the possibility that it was a fledgling that died at or near the nest. The description of the site as "under an overhanging rock and not in a proper cave" (Hector, in Haast 1874: 63) indicates that it was not a natural trap, so no conclusions can be drawn on the cause of death.

8.7.2.6 *Loess* A Haast's Eagle femur was reported from "a loess bed" in a gully near Hamilton Swamp, on the northwestern margin of the Rock and Pillar Range (Haast 1881). However, the report was second-hand and nothing more was recorded about the depth or stratigraphy of the deposit, so the mode of deposition is unknown.

The two sites at Cape Wanbrow were covered by deep loess deposits but these were not laid down until after the sand lenses which contained the eagle

material (Grant-Mackie & Scarlett 1973).

The only other mention of loess in connection with Haast's Eagle is a description in passing of the "turbary and loess deposits of Glenmark" (Haast 1881: 232). Here, the loess evidently alludes to the two deeply buried sites upstream from the main swamp deposits (see 8.2.2.6). In his earlier descriptions of these sites (Haast 1872, 1874, 1879; see 8.2.2.26), Haast stated that the bones were in peat layers; presumably the reference to loess at Glenmark relates to the silt layers in the strata covering the older deposits.

8.7.3 Rate of entrapment

The rate of entrapment of eagles would have depended on many factors. Some of these must have been the type of trap, its duration as a trap, local population size of both eagle and prey, the probability of an eagle's being trapped or dying in the trap when not hunting, the probability of potential prey being trapped, the probability of an eagle arriving before prey sank or ceased being conspicuous, and the probability that the eagle would be trapped while attacking or feeding on a particular individual. Operationally, calculation of a true rate depends on obtaining reliable estimates of all these factors, plus the probability of a diagnostic part of its body being preserved. An estimate of the rate therefore depends on the accuracy of MNI estimates for both predator and prey, good chronological control for the fossil sequence, and an estimate of rate of material loss or destruction during and after deposition.

Rates calculated for the well-dated deposits in Graveyard at Honeycomb Hill and in Pyramid Valley showed that swamps trapped eagles at a higher rate than did caves. In Graveyard, the ^{14}C dates suggest that eagle remains in Layer 3 were deposited over a period lasting from about 20 600 BP to 16 200 BP, or 4 200 years, and perhaps until 14 000 years BP (6 600 years) (Worthy 1987). Therefore, the five birds in Graveyard were deposited at minimum rates of one per 840 years (0.0012 yr^{-1}); or one per 1 100 years (0.00091 yr^{-1}). If only 20% of the birds that died in the cave over that time are represented in the sample (and MNI), the rate is still less than one per 160 years (<0.0063 yr^{-1}).

Four birds have been identified from Pyramid Valley (Table 8.7), and Burrows (1989) estimated that the lake may have acted as a trap for moas for about 1 300 years. A rough estimate of the minimum rate of entrapment for eagles would therefore be one per 325 years (0.00308 yr^{-1}), or about 2.5-3 times the rate for Graveyard. If a similar rate of attrition (20%) is assumed for Pyramid Valley, the rate would be about one per 65 years (0.0154 yr^{-1}).

The rate for Pyramid Valley is also likely to be an underestimate for two reasons: only part of the deposit has been excavated (see 8.2.2.26; Fig. 8.26C); and most moas may have been trapped over a much shorter time than the duration of the lake phase in Pyramid Valley. The *gyttja*, which accumulated at 0.45 mm $year^{-1}$ (Gregg 1972), would have taken some time to develop to a depth at which it could efficiently trap moas. Burrows (1989) pointed out that most of the ^{14}C dates for moas are for a period of about 250 years, between 3 500 and 3 750 years BP. For this period alone, the rate would then be nearer one per 60 years (0.0167 yr^{-1}), or one per 12 years (0.0835 yr^{-1}) allowing for attrition. If 40 rather than 4 eagles are present, then the rates would be 0.16-0.8 eagles yr^{-1}.

The average rate of entrapment in Graveyard was therefore up to an order of magnitude less than that at Pyramid Valley. The actual rates of entrapment probably fluctuated rather widely, and several sites (e.g., Glenmark Swamp and Castle Rocks) that contained the remains of two individuals of markedly different size, may have acted as a trap only once. It may be that these were mated pairs (see Chapter 2A for discussion of sexual size-dimorphism in *Harpagornis moorei*), and that they were trapped together, perhaps at the same carcase.

One reason that the rate of deposition (if not strictly entrapment) could have been higher in Pyramid Valley than in Graveyard, is that eagles probably died and fell into the lake or swamp in the normal course of events, as did other, non-predatory, birds (lists Scarlett 1955, 1969). This would have occurred more often at Pyramid Valley because the site surface was much larger than the entrances at Honeycomb Hill Cave, and birds would have been attracted to drink and to hunt prey attracted to the lusher vegetation around the lake.

Conversely, moas must have rarely survived falls into caves long enough to

have been noticed by eagles, which did not habitually search for prey in caves in their hunting range of several square kilometres.

8.8 DISCUSSION

8.8.1 General

A major problem in determining the distribution of Haast's Eagles is gauging how closely the distribution of fossil sites containing eagle bones mirrors that of the living bird. Obviously, late Quaternary fossil sites are not randomly distributed in New Zealand: there are more in the lowlands, and more where calcareous rocks provide suitable depositional environments (Anderson 1990). However, the fossil distribution of Haast's Eagle is not random with respect to the distribution of natural and archaeological fossil sites. Most well-dated sites from after 10 000 years BP are clustered in the east and south of the South Island, and only one is in the North Island.

The strongest argument in favour of the eastern South Island being the centre of distribution during the Holocene is the almost total absence of eagle material from similar sites elsewhere. For example, if the bird had been present in the northern North Island, or away from the coast in the southern North Island, its remains would be expected in the extensive dune sites of Tokerau and Waikuku Bays in Northland, in the Waikato caves, and in the lake and swamp deposits of Poukawa and Makirikiri. All have diverse fossil avifaunas, the result of extensive and intensive collections, but eagles have never been found there (Horn 1983; Millener 1981; Millener & Templer 1981; Scarlett 1979; Worthy 1984; Worthy 1990).

8.8.2 Physical environment

Differences in climate and/or physical environment between, for example, the rich fossil site of Tokerau Beach, and those at Cannibal Bay and Warrington on the southeastern coast of the South Island, are unlikely to have affected Haast's Eagle, because the eagle's range in the South Island included greater extremes of both. Northern sites are of similar age: Tokerau contained bones dated from

1 130±70 to 4 290±100 years BP (Millener 1981), a period that is well within the time span of the bird's presence at South Island sites, and the climate is equable in both and has not changed significantly in the past 5 000 years (Burrows 1979). Eagle bones have been found in seven dune sites in the South Island; the absence of material from northern North Island dune sites makes it unlikely that eagles could have been present when deposition was occurring. However, the Waingongoro specimen shows that birds were present in coastal southern Taranaki.

There appears to be little in the physical environment that can explain the absence of eagles from northern inland sites. Most are at low altitude, and in gentle terrain characteristic of much of the North Island away from the main eastern ranges. Six South Island sites are in karst, but sites in extensive areas of karst in the Waikato and Northland, although fossiliferous (Millener 1981; Millener & Templer 1981; Worthy 1984), have not yielded eagle bones.

Eagles lived in areas of both high and low precipitation, and at altitudes from sea level up to 1 600 m in the South Island. Poukawa in Hawke's Bay and Pyramid Valley in northern Canterbury are both in downland and are both subject to droughts and heavy seasonal rain. Although eagles seem to have been most abundant in the lower rainfall regions of the east and south of the South Island, their presence in high rainfall areas, on Mount Owen, Castle Rocks, and probably at Holyoake Stream within the past 3000 years, suggests that precipitation *per se* was not a limiting factor.

Other aspects of the physical environment are unlikely to have been directly responsible for limiting the bird's range. According to Coulter (1973) all of New Zealand except the high mountains and central Otago can be placed in one general climatic category, i.e. a temperate rainy climate with warm summers and no marked dry season. The range in mean annual temperature between the far north and Foveaux Strait is about 5°C (Coulter 1973: fig. 2.1b). Mean temperatures in the central Otago basins are similar to those on the adjacent coast and as far north as Cook Strait, but the extremes are far greater, and certainly exceed latitudinal differences. Large raptors of temperate regions in the northern hemisphere, such as the Golden Eagle, have distributions that

encompass much greater ranges of climatic conditions (Brown & Amadon 1968) than are encountered in New Zealand.

Wasser (1986) found that the resting metabolic rate of accipitrids from tropical habitats was lower than in birds from temperate climates. However, the species he studied were also found in temperate habitats, which suggests that species can acclimate to different temperature regimes.

The extinct hawk *Circus eylesi* Scarlett, 1953 has been found in natural and archaeological fossil sites in many areas of both islands inside and outside the known range of Haast's eagle (Scarlett 1953; Millener 1981), and there is no obvious climatic or physical factor which would have affected one bird but not the other.

Terrain and climate do not seem to be important factors affecting the distribution of other large raptors in temperate regions. The Wedge-tailed Eagle (*Aquila audax*) of Australia has a wide range of habitats "from mountain forests to nearly treeless plains" (Pizzey 1980: 84). The American Bald Eagle (*Haliaeetus leucocephalus*) is found mainly near lakes, rivers, and the sea coast, but its range includes the subtropical Florida Everglades and river valleys in Alaska and it winters on the Alaskan coast (Brown & Amadon 1968). Golden Eagles (*Aquila chrysaetos*) migrate from the more northerly parts of their range in winter, but those in Scotland move only to lower altitudes (Brown & Amadon 1968).

The absence, or at least rarity, of Haast's Eagle in the North Island Holocene and its relative abundance in the east and south of the South Island have to be explained instead by factors in the biotic environment.

8.8.3 Vegetation

The biotic factor about which most is known is the vegetation. Most eagle sites were in or near forest at the time bones were being deposited. An association with forest is not surprising, because most of the land area of New Zealand below the snowline was covered by some form of woody vegetation during the Holocene (McGlone 1988, 1989). However, New Zealand's Holocene forests varied from dense, wet rainforest typical of some North Island and West Coast forests today, to complex, drier, forest-shrubland mosaics on the eastern plains,

foothills, and central mountain basins (McGlone 1989). Holocene eagle sites are commonest in areas formerly covered by drier, more diverse, wooded habitats.

Wet lowland podocarp forest spread rapidly over most of the North Island after 14 000 years BP (McGlone 1988; Newnham *et al.* 1989). The forest cover in the far north, Waikato, inland Taranaki, the Manawatu, and inland Hawke's Bay thereafter remained largely intact until Polynesian fires removed large areas after 1 000 years BP (Dodson *et al.* 1988; Horn 1983; McGlone 1978; Newnham *et al.* 1989). Sites in small areas of coastal forest and shrubland in Northland were isolated by extensive lowland forests and lacked eagles; the exception is Waingongoro, on the southern Taranaki coast within sight of the South Island.

The few large fossil avifaunas from Holocene deposits on the West Coast of the South Island do not contain eagle remains (e.g., Metro Cave, Millener 1980). However, the clearest evidence that lowland wet forest did not support large populations of eagles is that eagles are not recorded in the Oparara cave deposits after 10 000 years BP. Here, in the same geographic area, a change to wet lowland forest around 10 000 years BP was accompanied by a change in the avifauna, including the dominant species of moas (Worthy & Mildenhall 1989). Before then, the vegetation was montane forest, with subalpine shrubland (Worthy & Mildenhall 1989) and eagles were common judging from their presence in sediments dating from the Otiran glacial maximum of 22 000-14 000 years BP and from the transitional period from 14 000 to 10 000 years BP.

Eagles may have been more widespread in the southern part of the North Island in Otiran times, when the vegetation was more diverse in structure (McGlone 1988). If Worthy (1987) is correct in assigning an Otiran age to the Te Aute deposits, then Haast's Eagle was present in inland Hawke's Bay in the Otiran but apparently absent during much, if not all, of the Holocene. The nearby Poukawa site has sediments dating from about 7 000 years BP to less than 1 000 years BP and the recorded avifauna is much richer than that at Te Aute; however, as noted above, eagles have not been recorded (Horn 1983).

Little is known about the vegetation at the other two North Island sites. The Hunterville deposit apparently dates from the Otiran (Millener 1981). If eagles had been present in the Manawatu area during the Holocene, it is

difficult to see why they would not have been represented in the collection from Makirikiri inland from Wanganui. Worthy (1990) pointed out that the number of moa bones retrieved from the springhole swamp were similar to the numbers from the richest South Island sites such as Kapua and Enfield. All the material was passed through sluice boxes, unlike the procedures adopted elsewhere, and it is unlikely that eagle bones would have been missed if they had been present. Although the Puketapu site is possibly Holocene in age, it may, like Te Aute, be Otiran.

The two South Island Holocene sites west of the Alpine Fault show that Haast's Eagle was not confined to drier forest-shrubland mosaics. On Mount Owen, the bird was living in subalpine grassland and herbfield, well above the treeline. At Holyoake Stream, the site was in lowland rainforest. Both sites are on karst, and Williams (1982) noted that Holyoake Stream is an example of a dry catchment where most of the stream flow is channelled underground. The valley forest may have not been typical of that elsewhere on Takaka Hill. [As noted in section 8.2.2.10, this site is probably to be identified with Hawkes Cave, near the top of Takaka Hill, and the deposit is probably late Pleistocene to early Holocene in age.]

8.8.4 Habitat versus ecology

The distribution of Haast's Eagle generally corresponded to that of drier forest-shrubland mosaic vegetation, but the bird was able to live in diverse habitats at a range of altitudes. The bird appears to have preferred terrain with a gentle relief, but the evidence is equivocal because fossil sites are rare in the main ranges.

The wide range of physical conditions and vegetation types inhabited by Haast's Eagle suggests that diet and the availability of prey were more important in limiting its distribution than was habitat. Prey abundance affects breeding success in many raptors (Newton 1979). Larger raptors have larger home ranges, presumably because they eat large prey; large prey species are less abundant than small species (Newton 1979). Variation in breeding density has been linked to territory qaulity, with higher densities of birds in areas with abundant prey,

and surpluses of prey during the breeding season (Newton 1979). Newton (1989) reported a clear relationship between lifetime breeding success and territory quality in the European Sparrowhawk (*Accipiter nisus*). Annual production for single pairs was also slightly higher in better territories (Newton 1989).

In a study of food-niche relationships and guild structure in birds of prey, Jaksić & Braker (1983) concluded that raptors were opportunistic in their food habits, but that they tend to kill the largest prey they can handle. Minimum prey size was probably determined by a need for a positive energy balance. However, Jaksić & Braker (1983) also found that the larger predators did not have more generalised food habits than smaller birds. They stressed that prey resources and diversity, and general cost-benefit trade-offs, were important for prey choice in accipitrids.

If the distribution of Haast's Eagle was not directly correlated with a specific habitat, and prey availability is an important determinant of bird of prey populations, one hypothesis relating the two factors is that the eagle's distribution was determined by the distribution of its potential prey. This hypothesis can be tested by examining the patterns of association of Haast's Eagle and other birds in the pre-human environment. A test of the hypothesis is the subject of Chapter 5.

Any link between the eagle's distribution and environmental conditions was probably a consequence of the preferred habitat of its prey, and the absolute abundance, availability, and vulnerability of prey.

8.8.5 Fossil sample analysis

The only direct clues to the abundance of Haast's Eagle in different areas, and to the faunas with which it was associated, are the fossils themselves. The eagle's presence and abundance in different kinds of site can also give insights into its behaviour and ecology. Such information is complementary to and independent of that derived from functional morphology.

The fossil sample of Haast's Eagle is comparatively large, and all elements of the skeleton are represented. The good preservation typical of most cave and some swamp sites meant that most limb bones could be measured. Used with

bone length proportions derived from known individuals, the measurements allowed a better assessment of minimum numbers of individuals (MNI) than would have been possible otherwise. The complete specimens were also important for the functional morphology and phylogenetic analyses in that Haast's Eagle could be treated as a living taxon.

Variation in contralateral limb bone lengths was low and similar to that for other large raptors (pers. obs.). The low variation is hardly surprising as it would be distinctly disadvantageous for a bird to be significantly bilaterally asymmetrical, particularly with respect to locomotory elements. Contralateral elements could be assigned confidently to individuals at most sites, although the possibility that a particular bone came from a different bird, otherwise unrepresented in the sample, could never be discounted. Samples from sites such as Enfield where more than two birds were known from limb bones, where one bird was represented by a single bone, and the others were almost identical in size but distinguishable by the number of ipsilateral elements, were the most difficult to assess.

The carpometacarpus was the most difficult element to assign because the contralateral variation was greater than in other elements. This variation was particularly noticeable in the smaller individual from Castle Rocks, but it is also possible that the material included one element from a third individual. Until the variation in length of contralateral carpometacarpi can be quantified more satisfactorily, that element should be used with care in the determination of MNI.

Using the protocol adopted here, the MNI index is probably as efficient as other maximum likelihood indicators of abundance (Holtzman 1979). An MNI index places a lower limit on the representation of a species in a sample; the upper limit is, potentially at least, set by the number of elements of that species in a sample. With increasing diversity of element type, the MNI index should approach closely the 'true' number of individuals present. As more different elements are recorded, it is more likely that a few individuals are well preserved in the sample, than it is that many are poorly represented.

The pattern of differential preservation in the total sample of Haast's

Eagle was similar to that found by Rich & Baird (1986) and Napawongse (1981) for birds. However, some differences were apparent. Napawongse (1981) used skeletons of a small seabird (*Pachyptila belcheri*) in tumbler experiments to measure the rate of attrition of each kind of element. In these experiments, whole skeletons were mixed in a rotary tumbler, and the degree of damage to each kind of element assessed at intervals until no recognisable elements remained. Limb bones survived best in both samples, but the survivability of crania and other axial elements was higher in Haast's Eagle than in Napawongse's sample. The higher survival of these elements in Haast's Eagle is probably related to the generally low-energy depositional environments characteristic of New Zealand cave deposits.

Very few eagles were represented by small fragile elements, and these were nearly always birds represented by other elements. This agrees with the pattern of early loss of fragile elements demonstrated by Napawongse (1981).

The low survival rate of small or delicate elements has two practical applications. In site surveys, larger elements should be sought. The presence of smaller elements is a good indication of a high quality site, once an initial survey is complete. Lists of elements should always be available to guide recovery excavations.

Most eagle sites showed little evidence of transport, but where this was apparent, as in Graveyard, His Cave, and Pyramid Valley, the elements were generally transported in the order suggested by Rich & Baird (1986). Ribs and vertebrae were amongst the rarest elements, and the main limb elements were found in roughly equal proportions, suggesting that they were moved from the carcase - and eroded - in no particular order. However, the sterna and crania at Pyramid Valley were apparently dispersed by flotation rather than by traction, probably because the animals decayed in shallow water with gentle wind-driven currents. The distortion apparent in the death position of the Mount Owen specimen indicates that the pectoral girdle separates from the carcase as a unit, presumably driven by the expansion of gases within the body cavity. If the vertebrae then separated, the two 'ends' of the body could then drift independently and drop elements over a wide area.

An important factor in the minimal transport and good preservation of cave material in New Zealand has been the absence until recently of rodents and other small scavenging mammals. The *kiore* (*Rattus exulans*) arrived about 1 000 years BP (Atkinson 1985); material deposited since then could have been fragmented and dispersed by this species, which, judging from the frequency of its remains, regularly entered caves. Some eagle elements had been gnawed by rats, and a weka moved material from the Mount Owen specimen. However, animal damage to bone deposits was usually restricted to trampling by newly trapped birds.

8.8.6 Entrapment

The mode and rates of entrapment give some indication of the habits of Haast's Eagle and its abundance in different areas. Cave sites trapped eagles less often than swamps, but the bones generally were better preserved in caves, and the caves operated as traps for longer periods.

At Castle Rocks and Glenmark, two birds of distinctly different size were preserved. If the sex ratio was about equal, which is normal in raptors (Newton 1989), the chances of each sex being trapped were also probably about equal. It has been suggested (e.g., Hamilton 1893) that the two birds found in the Castle Rocks fissure represented a pair which entered the trap to feed on the same carcase. An individual of each sex, as dissimilar-sized birds are likely to be (Holdaway 1990), in one site is, at best, equivocal evidence for hunting in pairs.

Much has been made of the presence of eagle remains in the same sites as those of moas and other large flightless birds (e.g., Duff 1949; Haast 1872; McCulloch 1982). My results do not support or refute a cause and effect relationship, at least for swamp sites. The number of eagles in swamps such as Pyramid Valley could easily have been reached by natural attrition of birds from resident populations, as is likely for the non-predatory birds found there.

Birds of prey are common in swamp and cave fossil faunas elsewhere. Most of the birds from the La Brea tarpits in California are raptors and Steadman & Martin (1984) assumed that the birds had been scavenging on carcases. However, they presented no evidence in support of this assumption apart from their being

as numerous as supposedly scavenging mammals such as the Dire Wolf (*Canis diris*). However, it is speculation that the the wolf was scavenging too. The La Brea raptors undoubtedly include some obligate carrion eaters, such as *Neophrontops* and *Neogyps*, but they also include *Spizaetus*, which is not known to scavenge dead carcases (Steadman & Martin 1984).

However, although some eagles preserved in caves may have fallen in accidentally, and the Mount Owen specimen almost certainly did, most were probably attracted to living prey trapped in the cave. Ballmann (1969, 1973) recorded fossil raptors from fissure deposits, and Arredondo (1976) suggested that the large fossil eagles and owls of Cuban cave deposits preyed on rodents and insectivores, rather than carrion.

8.8.7 Conclusions

The data presented here suggest that the distribution pattern of Haast's eagle based on fossil deposits mirrors the distribution of the living population rather than that of suitable sites for fossilisation.

There is also evidence that the eagle was not present throughout New Zealand during the Holocene, and that the distribution changed in synchrony with climatic and vegetation changes over the past 15 000 years. The distribution of Haast's Eagle seems not to have been governed by physical, topographical, and vegetation patterns, except insofar as these controlled the distribution of prey species.

Patterns of association between Haast's Eagle and other taxa in New Zealand fossil deposits are examined in Chapter 4.

CHAPTER 4

9. CHAPTER 4
HAAST'S EAGLE IN THE NEW ZEALAND PRE-HUMAN AVIFAUNA

9.1 INTRODUCTION

Haast's Eagle did not live in isolation. It was one species in a rich and diverse avifauna. Its role in that avifauna has been controversial since it was discovered 120 years ago (Duff 1949; Haast 1872; McCulloch 1982, 1991; Owen 1879). A description and discussion of the composition and structure of the pre-human avifauna is included here in an attempt to place Haast's Eagle in the context of a diverse, functioning ecosystem (Holdaway 1989, Chapter 4A).

Between 800 and 400 years BP, large areas of forest and shrubland communities in low rainfall areas of the east and south of the South Island were burned repeatedly and converted to grassland or stands of bracken fern (Molloy *et al.* 1963; Molloy 1969: McGlone 1988; McGlone 1989). Areas of the North Island were also deforested at this time (Dodson *et al.* 1988; McGlone 1988, 1989; Newnham *et al.* 1989). During the same period, many species of bird, including most of the largest flightless species, all the moas, and Haast's Eagle, went extinct (Cassels 1984; Holdaway 1989).

The extinctions resulted in a sharp decline in the diversity of the New Zealand avifauna over a few hundred years (Holdaway 1990b, Chapter 4B). The system of which Haast's Eagle was part collapsed. The two papers describing the pre-human avifauna and its vulnerability and collapse (Holdaway 1989, 1990) provide essential background for an analysis of the structure of the community in which Haast's Eagle lived.

In Chapter 3, I showed that physical environment and vegetation patterns were not directly correlated with the distribution of Haast's Eagle. I proposed that the bird's distribution was governed instead by the presence and abundance of suitable prey species. Unfortunately, the preferred prey is, of course, unknown, and it is still debated whether or not the eagle took live prey, or was primarily a scavenger (Holdaway 1989; McCulloch 1982, 1991; but see section 8.7.2.2 for evidence of active predation).

Knowledge of other eagles provides a framework for hypotheses on the likely prey and feeding strategy of Haast's Eagle. Large raptors tend to take large prey (Newton 1979). Jaksić & Braker (1983) concluded that raptors take all available prey from the largest that they can catch and kill, to the smallest that gives a positive energy balance. These limitations do not apply directly to carrion feeders, because the prey is already dead, but there are upper limits to the size of prey a carrion eater can gain entry to by itself (Brown & Amadon 1968). If Haast's Eagle was an obligate scavenger, it could have used carcases from the full range of New Zealand's flightless birds, up to and including *Dinornis giganteus* (DIGI).

If, however, the eagle caught and killed its own prey, there must have been limits to that prey's size. Harpy Eagles (*Harpia harpyja*) of South and Central America weigh up to 9 kg (Fowler & Cope 1964), and they have been seen to catch and carry off male howler monkeys (*Alouatta* sp.)(Peres 1990) that weigh up to 6 kg. The African Crowned Eagle (*Stephanoaetus coronatus*) is 25-30% of the Harpy's weight (Brown 1982), but kills and dismembers antelopes weighing up to 20 kg (Brown 1982). There would therefore appear to be no reason to suppose that Haast's Eagle could not have caught and killed some, at least, of New Zealand's larger flightless birds. These birds ranged in weight from less than 10 kg (the swan *Cygnus sumnerensis*) to over 250 kg for (*Dinornis giganteus*, Atkinson & Greenwood 1989; Holdaway 1989).

The hypotheses that the distribution of Haast's Eagle was limited by prey availability and abundance, and that the principal prey items were large flightless birds, led to the prediction that the distribution pattern of one or more species of flightless birds closely matched that of the eagle. If the distribution of the living birds corresponded to their fossil distribution, the composition of the fossil avifaunas should display coherent geographic and ecological patterns. One way of testing whether such patterns mean anything biologically is to compare them with associations and distributions of extant taxa represented in the fossil faunas.

The carrion/scavenger hypothesis predicts that Haast's Eagle would have been present anywhere there was a sufficient supply of carrion. It should not matter which species provided the carrion; carrion eaters are not prey specific

(Brown & Amadon 1968). Therefore, the hypothesis does not predict that the eagle was associated with any particular species or group of species of potential prey. Because there were no mammalian predators or scavengers in New Zealand, a carcase could have provided food, whether the eagle killed it or not, for at least several days, and possibly up to a week, especially during cooler weather, so even birds with a low population density could have provided food.

A strong association with one or a small group of potential prey species, with the same geographical distribution would both support the prey-limited distribution hypothesis and refute the carrion hypothesis. Conversely, if no clear pattern of association were to be found, the distribution hypothesis would be refuted and the carrion hypothesis corroborated.

To test the hypotheses, I first set out to show that the composition of the fossil bird assemblages contained ecological and geographical information. The presence or absence of a range of taxa with different habitat requirements over a range of sites from different areas, altitudes, and habitats should reflect the range of habitats and geographic replacement by related taxa.

Extant species with known ecologies could be used as indicator species for the habitats of extinct species in the same cluster or with similar loading on an ordination axis. The concept was formalised by Baird (1989) but had been in tacit use in New Zealand for many years, in the same way that mammals and invertebrates have been used for palaeoecological reconstructions elsewhere. Thus Yaldwyn (1958), Grant-Mackie & Scarlett (1973), and Worthy & Mildenhall (1989), amongst others, used the presence of small forest birds to infer the presence of forest at sites ranging in age from 2 000 to possibly 80 000 years BP.

Species lists were available for a wide range of sites of different ages, but to refine the analysis of associations between Haast's Eagle and the largest and best known group of potential prey species, the moas, I took advantage of the relative abundance data recently recalculated and presented by Worthy (1990).

9.2 METHODS

9.2.1 Samples Presence-absence data were abstracted from original literature sources where possible, with amendments to moa taxonomy as recommended by Worthy (1990). Lists from archaeological sites were derived mainly from Scarlett (1979), and are incomplete, but this is the best series of identifications available from one worker.

Two matrices were compiled. The first covered the whole fossil avifauna from 43 sites throughout New Zealand, and included presence-absence records of 98 species. The second matrix recorded presence-absence and relative abundance (% of total MNI) of all moa taxa and Haast's Eagle (MNI) at 26 sites. Abbreviated matrices are given in Table 9.1 and the full percentage representation data, eagle numbers, and information sources are given in Table 9.2. Four character taxon codes and alphanumeric site codes used in the figures are listed in Table 9.3.

Eagle minimum numbers of individuals (MNI) were included only with data on moa relative abundance. Worthy's (1990) identifications and reidentifications were based on 11 recognised species, synonymising *Dinornis torosus* with *Dinornis struthoides*, and new morphological information (Worthy 1987, 1988, 1989).

9.2.2 Statistical analysis

The composition of fossil avifaunas from natural and archaeological sites was analysed using Two-way Indicator Species Analysis (TWINSPAN), and Detrended Correspondence analysis (DECORANA) (Hill 1979; Hill & Gauch 1980).

Three different subsets of the data matrices were analysed: 98 species and 43 sites using presence-absence data; presence-absence of 11 moa species with and without *Harpagornis moorei* at 26 sites; and percentage representation of moa taxa with and without *Harpagornis moorei* at 26 sites. For each matrix, the clustering with respect to both sites and taxa was recorded as dendrograms (TWINSPAN). Loadings on the first three DECORANA axes were plotted in all combinations.

Table 9.1A (North Island) List of sites (sitecode: N, North Island) with bird species presence indicated by code numbers (see Table 9.3): used in TWINSPAN and DECORANA presence-absence analyses.

No.	Site	Species codes
N1	Waingongoro = Ohawe	44 7 4 52 57 102
N2	Te Aute	44 1 3 4 29 9 10 11
N3	Tangatupura	7 4
N4	Clevedon	1 7 4 9
N5	Kaupokonui	1 7 3 4 11 13 15 19 31 35 36 43 57 54 52 63 65 69 70 71 75 91 102 103 100
N6	Makirikiri	1 7 9 10 11
N7	Opua	1 7 3 4
N8	Poukawa	1 7 4 9 10 11 17 18 19 20 22 23 25 26 27 41 30 31 32 33 34 36 37 38 39 51 16 46 47 55 54 48 49 52 53 60 43 42 45 69 70 71 75 74 79 80 91 101 103 100
N9	Martinborough 1 and 5	1 9 13 41 57 52 48 70 45 103 93 69 73 76 101 91
N10	Paryphanta	13 48 52 53 70 71 75 81 97 99 93 94 109 90
N11	F1b	48 55 52 57 13 15 16 43 80 70 60 103 4 3 7 1 9 11
N12	F1c	48 55 52 57 13 15 16 71 70 69 33 41 29 103 101 84 87 97 60 3 7 1 9 10
N13	Washpool	3 47 48 55 54 49 53 57 79 71 70 74 75 69 82 93 91
N14	Tom Bowling Bay	13 15 20 19 23 31 43 46 48 55 52 58 59 63 65 68 67 69 70 71 75 79 80 90 91 103 100 9 4
N15	Waikuku Beach	13 23 43 46 48 58 63 65 69 70 103 100 42 66
N16	Houhora	27 100 1 4 3 9 11
N17	Opito	15 31 34 48 63 69 71 100 11 9 3
N18	Sarah's Gully	30 31 48 61 63 71 105 91 103 100 11 9
N19	Paremata	13 15 17 19 22 27 29 31 35 42 43 45 47 48 55 52 57 58 63 69 70 71 75 76 80 91 103 100 1 7 3 9 10 11
N20	Foxton	
N21	Makara	

Table 9.1A continued (South Island) List of sites (sitecode: S, South Island) with bird species presence indicated by code numbers (see Table 9.3): used in TWINSPAN and DECORANA presence-absence analyses.

No.	Site	Species codes
S1	Albury Park	8 5 9 11 44 53
S2	Castle Rocks	1 44 103 95 105 90 70 80 42 46 69 52 48 53 41 13 15 56
S3	Enfield	8 5 3 44 9 10 11 28 15 13 38
S4	Glenmark	8 5 3 44 9 10 11
S5	Hamilton	8 5 3 44 9 10 53
S6	Hamilton's	1 2 8 6 3 9 10 11
S7	Herbert	1 5 3 9 10
S8	Kapua	1 2 8 5 3 44 53
S9	Mount Owen	44 48 86 85 2 6 1 10 15 70
S10	Paerau	8 5 3 9 10
S11	Pyramid Valley	8 5 3 9 10 11 44 18 32 31 33 40 41 28 42 43 48 52 54 56 53 61 69 71 73 75 70 45 80 79 106 93 91 103 101 100 30 36
S12	Scaife's Lagoon	3 9 10 11
S13	Motunau	8 5 3 10 44
S14	Old Rifle Butts f/1212	44 8 19 31 36 28 41 30 45 56 46 48 63 67 69 75 71 73 70 80 93 100 101
S15	Oparara Graveyard L3	44 2 5 6 10 41 43 45 46 56 48 54 52 47 72 80 81 93 103 100
S16	Oparara Graveyard L1,2	1 2 41 35 33 43 46 56 48 54 60 70 72 80 81 85 86 88 93 91 101 103 106 100
S17	Ngapara	44 100 52 53 56 16 41 28 69 48
S18	Sumner	3 69 44 1 8 11 13 27 31 32 45 48 56 63 71 73 75 105 91 53
S19	Oparara Graveyard L4	2 6 28 41 56
S20	Eagle Roost	2 9 15 19 28 41 44 46 48 54 60 70 72 81 83 84 85 86 88 89 105 98 96 92 99 94 93 90 101 103 100 76 16
S21	Oaro	44
S22	Kakanui Beach	44
S22	Heaphy River Mouth	1 71 73 69 91 20
S23	Marfells Beach	13 17 18 110 19 22 27 28 30 31 33 36 41 38 37 44 42 43 45 46 47 48 54 52 56 53 60 61 63 65 68 67 69 70 71 73 75 76 79 80 93 91 101 103 106 100 8 3 1

Table 9.1B List of sites, by code (see Table 9.1A), with proportional representation of moa taxa and MNI for Haast's Eagle (Code 44) given in consecutive species code - percentage species representation pairs. Species codes as in Table 9.3.

No.	Species percentage/MNI
N1	7 16 4 67 11 1 44 1
N2	1 2.5 3 15.0 4 45.0 9 15.0 10 7.5 11 15.0 44 1
N3	7 50 4 50
N4	1 60.6 7 6.1 4 30.3 9 3.0
N5	1 19 7 17 3 8 4 53 11 3
N6	1 64.0 7 8.5 9 7.1 10 16.6 11 3.9
N7	1 18 7 27 3 9 4 45
N8	1 17.3 7 64.2 4 3.7 9 7.4 10 3.7 11 3.7
N19	1 69 7 8 3 4 9 8 10 8 11 4
N20	1 30 7 24 3 3 4 33 10 6 11 3
N21	1 25 7 25 4 37 10 13
S1	8 55.7 5 36.2 9 3.3 11 4.9 44 1
S2	1 100 44 2
S3	8 52.4 5 12.8 3 25.5 9 5.2 10 1.1 11 3.0 44 3
S4	8 57.0 5 15.3 3 11.8 9 8.3 10 2.1 11 5.5 44 2
S5	8 19.2 5 31.1 3 34.1 9 10.8 10 4.8 44 2
S6	1 7.5 2 2.5 8 15.0 6 2.5 3 12.5 9 12.5 10 15.0 11 5.0
S7	1 29.7 5 11.1 3 40.7 9 7.4 10 11.1
S8	1 0.5 2 0.5 8 33.3 5 8.4 3 20.8 9 7.3 10 5.2 11 4.0 44 1
S9	2 50 6 50 44 1
S10	8 5.0 5 51.7 3 14.6 9 1.5 10 0.5
S11	8 36.6 5 10.4 3 12.2 9 2.4 10 4.9 11 33.5 44 4
S12	3 41.7 9 41.7 10 8.3 11 8.3
S13	8 2 5 90 3 2 10 2 44 2
S15	2 67.9 6 26.8 5 3.6 9 0.9 10 0.9 44 16
S16	1 33.3 2 66.7

Table 9.2A Percentage representation of moa taxa at selected sites of Pleistocene and Holocene age, with and without known eagle association. Is, North (N) or South (S) Island. T, site type - SS, swamp springhole; SL, swamp lake; SP, swamp peat; C, cave; CF, cave fissure; CP, cave pothole; A, archaeological site; D, dunes; B, beach; AD, archaeological or dune. Codes for moa taxa: MEDI, *Megalapteryx didinus*; ANDI, *Anomalopteryx didiformis*; EMCR, *Emeus crassus*; *Pachyornis australis*; *Pachyornis elephantopus*; *Pachyornis mappini*; EUGE, *Euryapteryx geranoides*; EUCU, *Euryapteryx curtus*; DIST, *Dinornis struthoides*; DINO, *Dinornis novaezealandiae*; DIGI, *Dinornis giganteus*. Eagle, *Harpagornis moorei* present (number) or absent (-) at site; Veg, dominant vegetation at site - F, forest; FE, forest edge; CF, coastal forest; MF, montane forest; SH, shrubland; SA, subalpine. +, indicates presence in small numbers, divided into equal proportions of the residual percentage representation for analysis. Sources (Ref): 1, Haast (1879); 2, McKay (1882); 3, Grant-Mackie & Scarlett (1973); 4, Worthy (1987); 5, Worthy (1990); 6, Worthy & Mildenhall (1989); 7, Hamilton ((1893); 8, Worthy (1989). Continued on next page. See also Table 9.2B.

Site/age	I	T	Ref	Veg	Eagle	DIST	DINO	DIGI
PRE-OTIRAN								
Glenmark Creek 1	S	S	1	F?	1			
Glenmark Creek 2	S	S	1	F?	1			
Motunau	S	SP	2	F	2		+	
Old Rifle Butts	S	B	2	FE	1			
Cape Wanbrow	S	B	3	FE	1			
OTIRAN								
Tangatupura	N	S	4	?	-			
Te Aute no. 2	N	SL	5	SH	1	15.0	7.5	15.0
Oparara	S	C	6	SHMF	16	0.9	0.9	
HOLOCENE								
Clevedon	N	SS	5	F	-	3.0		
Coonoor	N	CP		F	-			
Foxton	N	A	5	CF	-		6	3
Kaupokonui	N	A	5	CF	-			3
Makara	N	A	5	CF	-		13	
Makirikiri	N	SS	5	F	-	7.1	16.6	3.9
Opua	N	A	5	CF	-			
Paremata	N	A	5	CF	-	8	8	4
Lake Poukawa	N	SL	5	F	-	7.4	3.7	3.7
Waingongoro	N	AD	5	CF	1			3.36

Table 9.2A continued Percentage representation of moa taxa at selected sites of Pleistocene and Holocene age, with and without known eagle association. Is, North (N) or South (S) Island. T, site type - SS, swamp springhole; SL, swamp lake; SP, swamp peat; C, cave; CF, cave fissure; CP, cave pothole; A, archaeological site; D, dunes; B, beach; AD, archaeological or dune. Codes for moa taxa: MEDI, *Megalapteryx didinus*; ANDI, *Anomalopteryx didiformis*; EMCR, *Emeus crassus*; *Pachyornis australis*; *Pachyornis elephantopus*; *Pachyornis mappini*; EUGE, *Euryapteryx geranoides*; EUCU, *Euryapteryx curtus*; DIST, *Dinornis struthoides*; DINO, *Dinornis novaezealandiae*; DIGI, *Dinornis giganteus*. Eagle, *Harpagornis moorei* present (number) or absent (-) at site; Veg, dominant vegetation at site - F, forest; FE, forest edge; CF, coastal forest; MF, montane forest; SH, shrubland; SA, subalpine. +, indicates presence in small numbers, divided into equal proportions of the residual percentage representation for analysis. Sources (Ref): 1, Haast (1879); 2, McKay (1882); 3, Grant-Mackie & Scarlett (1973); 4, Worthy (1987); 5, Worthy (1990); 6, Worthy & Mildenhall (1989); 7, Hamilton ((1893); 8, Worthy (1989). See also Table 9.2B.

Site/age	Is	T	Source	Veg	Eagle	DIST	DINO	DIGI
HOLOCENE								
Albury Park	S	SC	5	F	1	3.3		4.9
Castle Rocks	S	CF	7	F	2	5.2	1.1	3.0
Enfield	S	SS	5	F	3	8.3	2.1	5.5
Glenmark	S	SL	5	F	2	10.8	4.8	
Hamilton	S	SS	5	FSH	2	12.5	15.0	5.0
Hamilton's	S	SS	5	F?	-	7.4	11.1	
Herbert	S	SS	5	F	-	7.3	5.2	4.0
Kapua	S	SS	5	F	1			
Mount Owen	S	CP	8	SA	1			
Oparara	S	CP	6	F	-	1.5	0.5	
Paerau	S	SS	5	F?	-	2.4	4.9	33.5
Pyramid Valley	S	SL	5	F	4	41.7	8.3	8.3
Scaife's Lagoon	S	SL	5	F	-			

Table 9.2B Percentage representation of moa taxa at selected sites of Pleistocene and Holocene age, with and without known eagle association. Is, North (N) or South (S) Island. T, site type - SS, swamp springhole; SL, swamp lake; SP, swamp peat; C, cave; CF, cave fissure; CP, cave pothole; A, archaeological site; D, dunes; B, beach; AD, archaeological or dune. Codes for moa taxa: MEDI, *Megalapteryx didinus*; ANDI, *Anomalopteryx didiformis*; EMCR, *Emeus crassus*; *Pachyornis australis*; *Pachyornis elephantopus*; *Pachyornis mappini*; EUGE, *Euryapteryx geranoides*; EUCU, *Euryapteryx curtus*; DIST, *Dinornis struthoides*; DINO, *Dinornis novaezealandiae*; DIGI, *Dinornis giganteus*. Eagle, *Harpagornis moorei* present (number) or absent (-) at site; Veg, dominant vegetation at site - F, forest; FE, forest edge; CF, coastal forest; MF, montane forest; SH, shrubland; SA, subalpine. +, indicates presence in small numbers, divided into equal proportions of the residual percentage representation for analysis. Continued on next page. See also Table 9.2A.

Site/age	MEDI	ANDI	EMCR	PAAU	PAEL	PAMA	EUGE	EUCU
PRE-OTIRAN								
Glenmark Creek 1								
Glenmark Creek 2								
Motunau			+		90		+	
Old Rifle Butts								
Cape Wanbrow								
OTIRAN								
Tangatupura						+		+
Te Aute no. 2		2.5					15.0	45.0
Oparara	67.9			26.8	3.6			
HOLOCENE								
Clevedon		60.6				6.1		30.3
Coonoor								
Foxton		30				24	3	33
Kaupokonui		19				17	8	53
Makara		25				25		37
Makirikiri		64.0				8.5		
Opua		18				27	9	45
Paremata		69				8	4	
Lake Poukawa		17.3				64.2		3.7
Waingongoro						16		67

Table 9.2B continued Percentage representation of moa taxa at selected sites of Pleistocene and Holocene age, with and without known eagle association. Is, North (N) or South (S) Island. T, site type - SS, swamp springhole; SL, swamp lake; SP, swamp peat; C, cave; CF, cave fissure; CP, cave pothole; A, archaeological site; D, dunes; B, beach; AD, archaeological or dune. Codes for moa taxa: MEDI, *Megalapteryx didinus*; ANDI, *Anomalopteryx didiformis*; EMCR, *Emeus crassus*; *Pachyornis australis*; *Pachyornis elephantopus*; *Pachyornis mappini*; EUGE, *Euryapteryx geranoides*; EUCU, *Euryapteryx curtus*; DIST, *Dinornis struthoides*; DINO, *Dinornis novaezealandiae*; DIGI, *Dinornis giganteus*. Eagle, *Harpagornis moorei* present (number) or absent (-) at site; Veg, dominant vegetation at site - F, forest; FE, forest edge; CF, coastal forest; MF, montane forest; SH, shrubland; SA, subalpine. +, indicates presence in small numbers, divided into equal proportions of the residual percentage representation for analysis. See also Table 9.2A.

Site/age	MEDI	ANDI	EMCR	PAAU	PAEL	PAMA	EUGE	EUCU
HOLOCENE								
Albury Park			55.7		36.2			
Castle Rocks		100						
Enfield			52.4		12.8	25.5		
Glenmark			57.0		15.3	11.8		
Hamilton			19.2		31.1	34.1		
Hamilton's	2.5	7.5	15.0	2.5		12.5		
Herbert		29.7			11.1	40.7		
Kapua	0.5	0.5	33.3		8.4	20.8		
Mount Owen	+			+				
Oparara	66.7	33.3						
Paerau			5.0		51.7	14.6		
Pyramid Valley			36.6		10.4	12.2		
Scaife's Lagoon						41.7		

Table 9.3 List of acronyms and species names for bird taxa used in TWINSPAN and DECORANA analyses.

1, **ANDI** *Anomalopteryx didiformis* ; 56, APOT *Aptornis defossor*; 2, **MEDI** *Megalapteryx didinus*; 57, APDE *Aptornis otidiformis*; 3, **EUGE** *Euryapteryx geranoides*; 58, HAOS *Haematopus ostralegus*; 4, **EUCU** *Euryapteryx curtus*; 59, CHBI *Charadrius bicinctus*; 5, **PAEL** *Pachyornis elephantopus*; 60, 7, **PAMA** *Pachyornis mappini*; 62, HINO *Himantopus novaezealandiae*; 8, **EMCR** *Emeus crassus*; 63, LADO *Larus dominicanus*; 9, **DIST** *Dinornis struthoides*; 64, LABU *Larus bulleri*; 10, **DINO** *Dinornis novaezealandiae*; 65, LANO *Larus novaehollandiae*; 11, **DIGI** *Dinornis giganteus*; 66, STAL *Sterna albostriata*; 12, MOSP *Moa species*; 67, STST *Sterna striata*; 13, APAU *Apteryx australis*; 68, STCA *Sterna caspia*; 14, APHA *Apterys haasti*; 69, HENO *Hemiphaga novaeseelandiae*; 15, APOW *Apteryx oweni*; 70, STHA *Strigops habroptilus*; 16, APSP *Apteryx* species; 71, NEME *Nestor meridionalis*; 17, POCR *Podiceps cristatus*; 72, NENO *Nestor notabilis*; 18, PORU *Podiceps rufopectus*; 73, NENS *Nestor* n sp,; 19, PHCA *Phalacrocorax carbo*; 74, CYAU *Cyanoramphus auriceps*; 20, PHVA *Phalacrocorax varius*; 75, CYNO *Cyanoramphus novaezealandiae*; 21, PHSU *Phalacrocorax sulcirostris*; 76, CYSP *Cyanoramphus* species; 22, PHME *Phalacrocorax melanoleucos*; 77, CHLU *Chrysococcyx lucidus*; 23, EGAL *Egretta alba*; 78, EUTA *Eudynamys taitensis*; 24, EGSA *Egretta sacra*; 79, NINO *Ninox novaeseelandiae*; 25, BOPO *Botaurus poiciloptilus*; 80, SCAL *Sceloglaux albifacies*; 26, IXNO *Ixobrychus novaezealandiae*; 81, MENO *Megaegotheles novaezealandiae*; 27, CYSU *Cygnus sumnerensis*; 82, HASA *Halcyon sancta*; 28, CNCA *Cnemiornis calcitrans*; 83, ACCH *Acanthisitta chloris*; 29, CNGR *Cnemiornis gracilis*; 84, XELO *Xenicus longipes*; 30, TAVA *Tadorna variegata*; 85, XEGI *Xenicus gilviventris*; 31, ANSU *Anas superciliosa*; 86, TRLY *Traversia lyalli*; 32, ANGI *Anas gibberifrons*; 87, PAJA *Pachyplichas jagmi*; 33, ANAU *Anas aucklandica*; 88, PAYA *Pachyplichas yaldwyni*; 34, ANRH *Anas rhynchotis*; 89, DESP *Dendroscansor decurvirostris*; 35, HYMA *Hymenolaimus malacorhynchos*; 90, ANME *Anthornis melanura*; 36, AYNO *Aythya novaeseelandiae*; 91, PRNO *Prosthemadera novaeseelandiae*; 37, MEAU *Mergus australis*; 92, GEIG *Gerygone igata*; 38, BIDE *Biziura delautouri*; 93, PEAU *Petroica australis*; 39, OXSP *Oxyura* species; 94, PEMA *Petroica macrocephala*; 40, MASC *Malacorhynchus scarletti*; 95, PESP *Petroica* species; 41, EUFI *Euryanas finschi*; 96, MOOC *Mohoua ochrocephala*; 42, CIAP *Circus approximans*; 97, MOAL *Mohoua albicilla*; 43, CIEY *Circus eylesi*; 98, MONO *Mohoua novaeseelandiae*; 44, **HAMO** *Harpagornis moorei*; 99, RHFU *Rhipidura fuliginosa*; 45, FANO *Falco novaeseelandiae*; 100, COMO *Corvus moriorum*; 46, CONO *Coturnix novaeseelandiae*; 101, PHCA *Philesturnus carunculatus*; 47, GAPH *Gallirallus philippensis*; 102, HEAC *Heteralocha acutirostris*; 48, GAAU *Gallirallus australis*; 103, CACI *Callaeas cinerea*; 49, POTA *Porzana tabuensis*; 104, MEPU *Megalurus punctata*; 50, POPU *Porzana pusilla*; 105, ANNO *Anthus novaeseelandiae*; 51, POPO *Porphyrio porphyrio*; 106, TUCA *Turnagra capensis*; 52, POMA *Porphyrio mantelli*; 107, TUTA *Turnagra tanagra*; 53, FUCH *Fulica chathamensis*; 108, DISP *Dinornis* species; 54, GAHO *Gallinula hodgenorum*; 109, NOCI *Notiomystis cincta*; 55, CAKA *Capellirallus karamu*; 110, PENO *Pelecanus novaezealandiae*.

Numbers on dendrograms indicate the number of sites or taxa at each division. Indicator species for positive and negative branches are given in species code, and eigenvalues for each division level are given along the relevant branch. Eigenvalues are a measure of the amount of variance in the data accounted for at each cluster point.

DECORANA loadings reflect the residual variation in the data after correlated trends have been removed. Variance in the original data is reduced to dimensions along, in this instance, three axes.

9.3 RESULTS

9.3.1 General

The presence/absence of 98 taxa at 43 sites is summarised in Table 9.1A, and the percentage representation of moa taxa at North and South Island sites of various ages are given in Table 9.1B.

Cosmopolitan refers to taxa found on both main islands.

9.3.2.1 All taxa; 43 sites

TWINSPAN

Sites

Presence-absence (Fig. 9.1). Archaeological and natural sites were represented in three of the four second division branches of the dendrogram.

The first division separated sites on the basis of diversity, with sites with higher species number on the positive branch. Indicator species for the negative branch (*Gallirallus australis*, *Strigops habroptilus*, *Hemiphaga novaeseelandiae*) were all birds of damp forests. The first division within the group of 24 higher diversity sites consisted of eight wetter South Island, and one North Island, natural sites. The North Island site, Paryphanta, was separated at the third division. The 16 sites on the other branch were from drier eastern and northern areas, but included a pair of subsites from a Waikato cave (F1b, F1c).

The 19 sites on the positive branch at the first division were separated geographically at the second division by North and South Island endemics, and

some cosmopolitan taxa were better represented at North Island sites. Makirikiri was borderline in the separation.

The third division on the negative branch differentiated between northern, mainly coastal, sites and southern North Island, eastern, and coastal South Island sites. The basic separation by island was influenced by habitat effects, with Poukawa and Washpool being grouped with Marfells and Pyramid Valley because they share a range of freshwater taxa; the human site at Heaphy was intermediate. In contrast, the eight positive branch sites included many coastal taxa or showed evidence of filtering of representation by cultural or cave deposition regimes; preferred food species were more abundant at cultural sites, and flightless taxa were selectively sampled by most caves.

The third division on the main positive branch (19 species) separated northern and southern inland sites from a suite centred in Canterbury. All but one of the Canterbury group contained *Harpagornis moorei*.

Fourth division differences on the two main branches were based on geography (Coromandel sites v other North Island; Heaphy v eastern South Island) or taxa (Ohawe and Tangatupura v Clevedon, Makirikiri, Opua).

Species

Presence-absence (Fig. 9.2). The first division separated all but one of the moas, three waterbirds, and *Harpagornis moorei* from all other taxa.

Two large taxa (*Pachyornis australis* (PAAU), *Cnemiornis calcitrans* (CNCA)) were in few sites and were separated by the second division on the negative branch (83 species, Fig. 9.2). At the third division on this branch, the taxa were divided into one group containing primarily forest birds and another with both forest and freshwater birds.

Lower order divisions of the main positive branch included are not reported because the associations among moas and between moas and *Harpagornis moorei* are considered separately (Fig. 9.7). Fourth divisions on the main negative branch may reflect ecological differences. Water and forest taxa were further divided into freshwater (27 species) and coastal groups (17 species), with an admixture of forest species abundant at coastal archaeological sites.

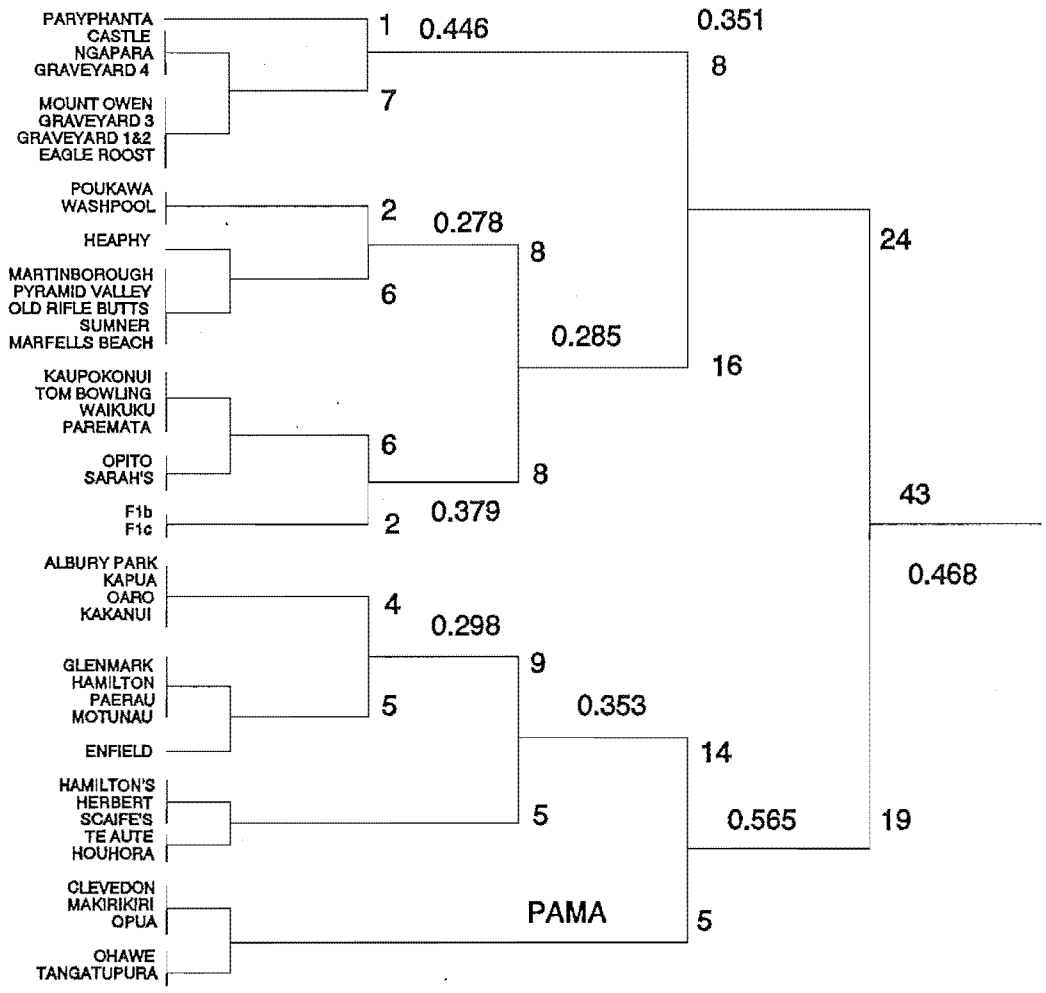

Fig. 9.1 TWINSPAN analysis of all sites, using presence-absence data (see Table 9.1A).

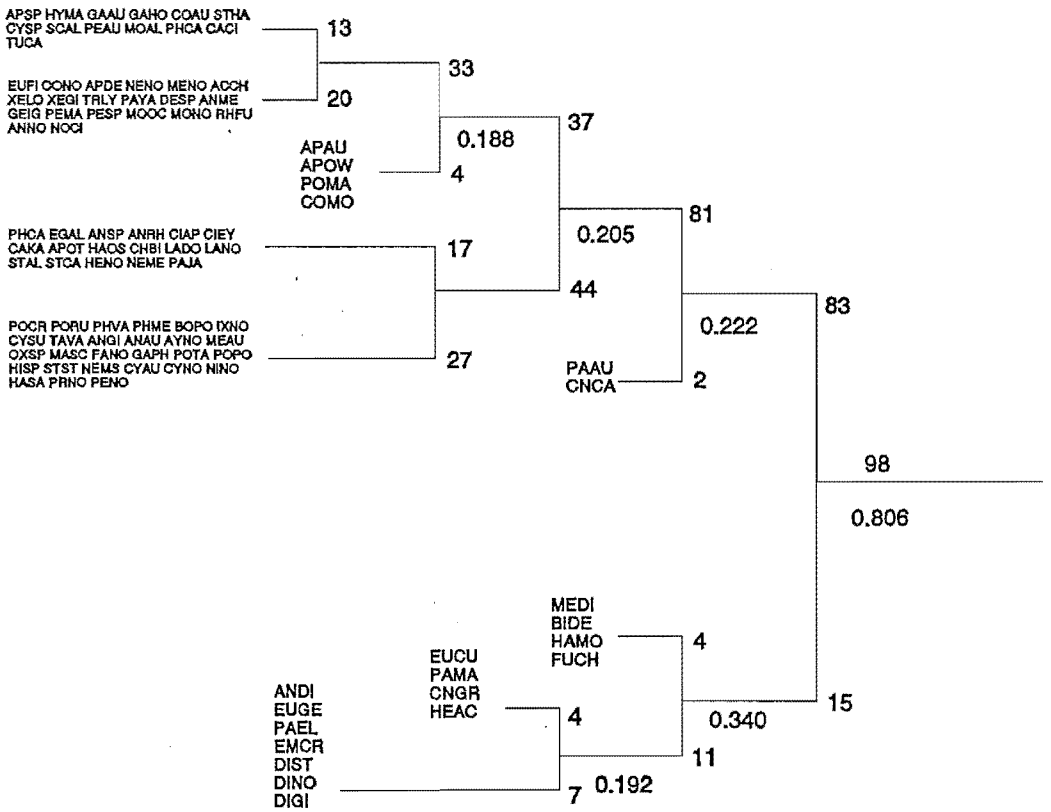

Fig. 9.2 TWINSPAN analysis of all taxa, using presence-absence data (see Table 9.1A).

Porphyrio mantelli (POMA) clustered with a group of three lowland forest taxa (*Apteryx australis* (APAU), *Apteryx oweni* (APOW), *Corvus moriorum* (COMO)). The remaining 33 taxa formed two branches that may reflect damper (13 species) and drier (20 species) sites, but the division is not clearly marked.

DECORANA

Sites

Presence-absence (Fig. 9.3). The eigenvalues declined regularly (0.485, 0.322, 0.189), suggesting that most of the species-composition was described by axes 1 and 2. However, loadings on axis 3 did separate sites with medium loadings on axis 1 and the upper range of axis 2.

Sites with low loadings on axis 1 had more species and were generally well separated from the sites with fewer species and higher loadings. In both groups, there was a south to north trend with increased loading on axis 2. Axis 1 appeared to reflect taphonomic effects, and axis 2 geographic or latitudinal effects, with northern sites having the higher loadings. The latitudinal discrimination was, however, complicated by altitudinal effects.

Axis 3 loadings were higher for sites with fewer freshwater or coastal taxa. Low loadings on axis 3, combined with the high diversity associated with low loadings on axis 1 resulted in sites with the most complex environment clustering in the lower lefthand corner of the scattergram.

Environmental effects were shown most clearly in the plot of axis 3 against axis 2. Here, the diversity-taphonomic effects traced by axis 1 are absent, and the latitudinal and altitudinal influences are balanced against ecological effects. Higher altitude and older sites are more common in the high 3/low 2 quadrant, and coastal sites cluster in the opposite low 3/ high 2 quadrant.

Species

Presence-absence (Fig. 9.4). Higher loadings on axis 1 corresponded to species more commonly found alone or with few other species. Axis 2 reflected a trend from low loadings for species more characteristic of inland sites to higher loadings for freshwater and coastal birds and some forest species. Superimposed

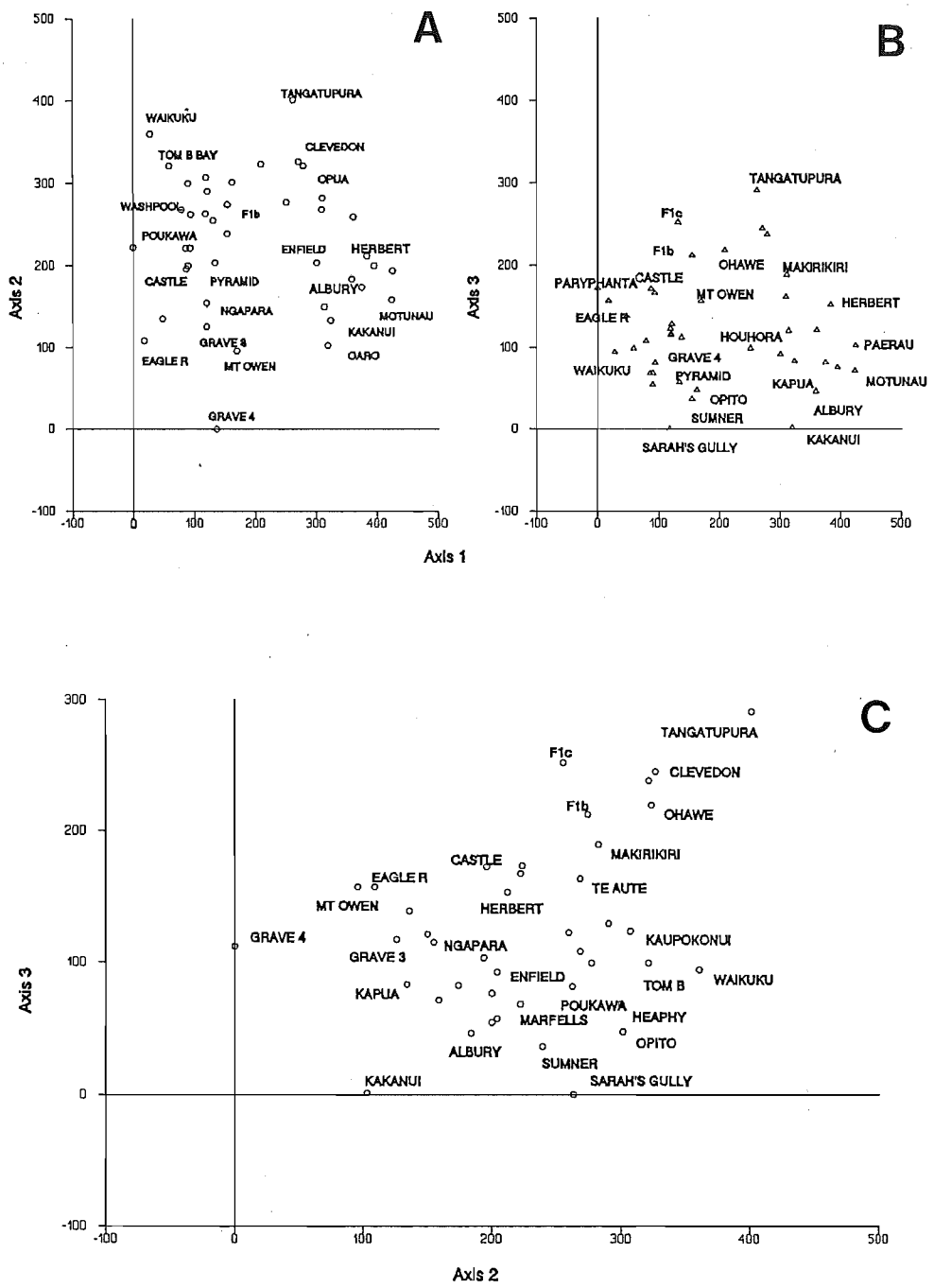

Fig. 9.3 Position of sites on first three axes of the ordination using Detrended Correlation Analysis (DECORANA): A, xis 2 v axis 1; B, axis 3 v axis 1; C, axis 3 v axis 2. Axes are scaled in s.d. units.

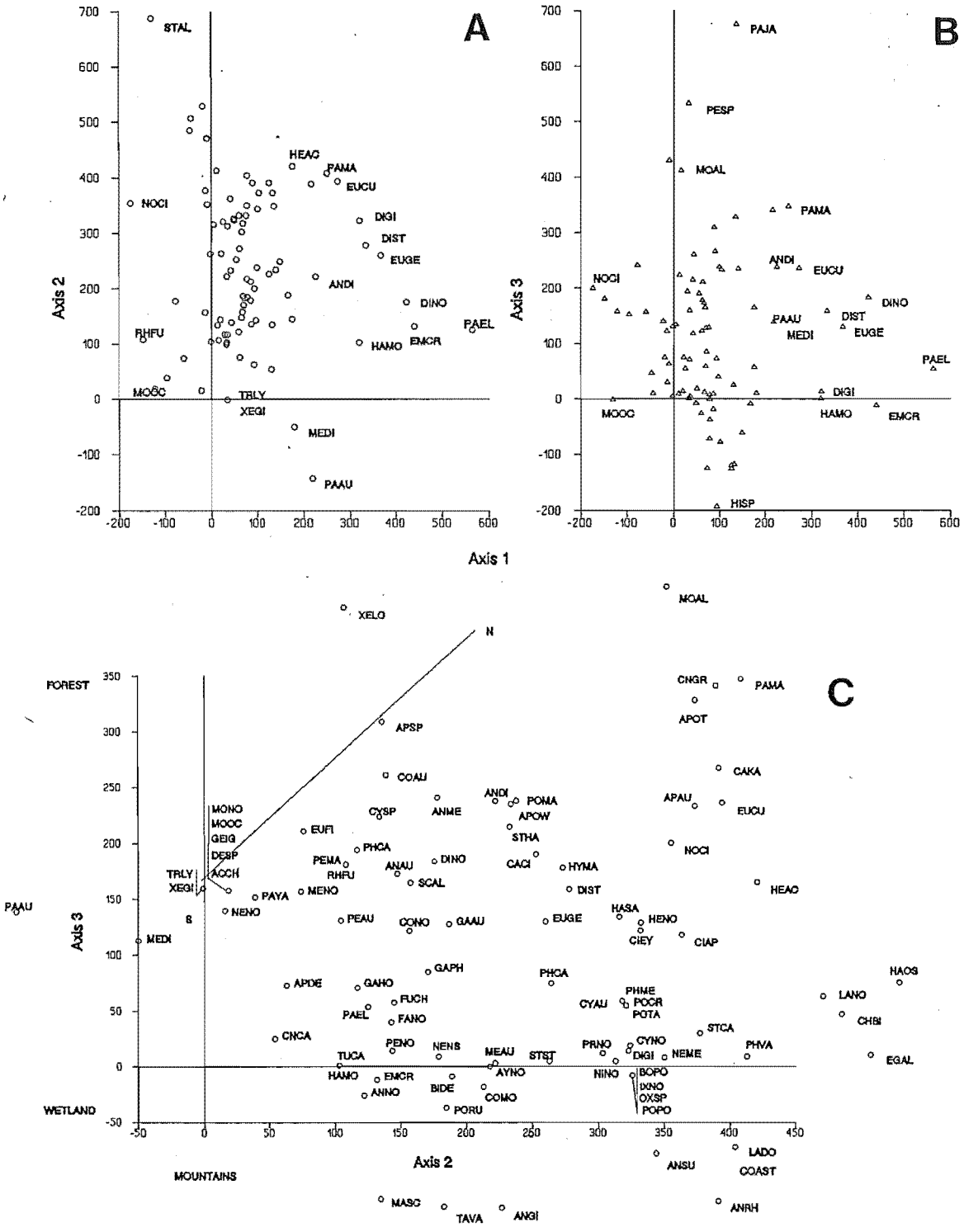

Fig. 9.4 Position of taxa on first three axes of the ordination using DECORANA: A, axis 2 v axis 1; B, axis 3 v axis 1; C, axis 3 v axis 2 (note expanded scale). See Table 9.3 for species acronyms.

on the altitudinal trend was a slight latitudinal gradient; low loadings suggesting a predominance of southern taxa. An increasing spread is apparent on axis 2 with lower axis 1 loadings, indicating that species from several different habitats were sampled at the more diverse sites.

High loadings on axis 3 were for species from purely forest sites; freshwater or coastal species had the lowest loadings. Habitat complexity appeared to be greater in lowland environments, where there were more lakes and streams.

The diversity components of axis 1 were reduced in the plot of axis 3 against axis 2. Taxa appeared to be segregated into broad ecological groups. Forest taxa, and those of the interior uplands occupied the top left quadrant, grading through progressively more complex environments with more freshwater habitats, to coastal associations at the lower right. Some forest birds (e.g., *Nestor meridionalis* (NEME), *Cyanoramphus novaezelandiae* (CYNO), *Cyanoramphus auriceps* (CYAU), *Prosthemadera novaeseelandiae* (PRNO)) appeared within the coastal group, probably as a result of their presence in several coastal archaeological sites.

9.3.3.2 11 moas and eagle; 26 sites

TWINSPAN

Sites

Presence-absence (Fig. 9.5). The main division was geographical, between the North and South Islands. Te Aute was carried into the southern group, presumably because of its Pleistocene age with resulting absence of the northern taxa *Pachyornis mappini* (PAMA) and *Euryapteryx curtus* (EUCU). *Pachyornis mappini* (PAMA) was the indicator species for the North Island group and *Pachyornis elephantopus* (PAEL) for the South Island.

The second division branches in the southern and northern groups were based on the presence of the *Euryapteryx geranoides* (EUGE)-*Emeus crassus* (EMCR) species-pair and the absence of *Anomalopteryx didiformis* (ANDI), respectively.

Three coastal sites from southern Taranaki and the Manawatu were

separated at level three from others containing *Anomalopteryx didiformis* (ANDI), by having *Euryapteryx geranoides* (EUGE) but lacking *Dinornis struthoides* (DIST). The larger group included inland sites and others adjacent to hill country to the north and south.

In the South Island, *Pachyornis elephantopus* (PAEL) was characteristic of a group of eastern sites, which were further divided by the presence orabsence of *Harpagornis moorei*. *Anomalopteryx didiformis* (ANDI) and *Megalapteryx didinus* (MEDI) defined a group of two southern South Island sites with a North Island, Pleistocene site.

Relative abundance (Fig. 9.6). The distribution of sites within the dendrogram and the indicator species were the same as for presence-absence data, except: the Oparara-Castle Rocks-Mount Owen suite was further resolved; and Albury was separated from the Enfield-Glenmark-Pyramid suite.

Species

Presence-absence (Fig. 9.7A). The first division was geographic, separating a group of two North Island endemics and two cosmopolitan species from the rest. The second division was again based on distribution, separating the three other cosmopolitans from South Island endemics plus *Harpagornis moorei*. The geographic base to the third division could be interpreted as an altitudinal effect rather than a latitudinal one, with *Megalapteryx didinus* (MEDI) and *Pachyornis australis* (PAAU) being better represented at upland sites, and *Pachyornis elephantopus* (PAEL) and *Emeus crassus* (EMCR) being commoner nearer the coast or inland in the south.

Relative abundance (Fig. 9.7B). The first division separated the two North Island endemics and the cosmopolitan *Anomalopteryx didiformis* (ANDI) from the rest. The three cosmopolitan dinornithids were separated together at the next division. Groupings of the remaining taxa appeared to reflect ecological as well as geographical effects. The *Pachyornis elephantopus* (PAEL)-*Emeus crassus* (EMCR) pair was more typical of southern coastal and inland basin sites.

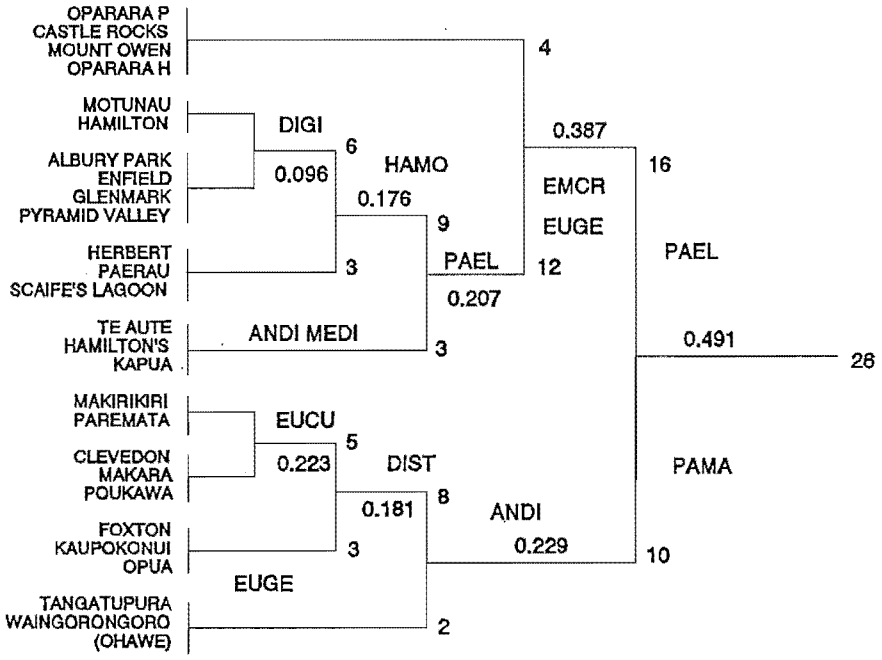

Fig. 9.5 Classification of sites using TWINSPAN (Two-way Indicator Species Analysis) on presence-absence data (Table 9.1A). Oparara P, H: Pleistocene or Holocene-aged sites. (Species acronyms Table 9.3). Other conventions in text.

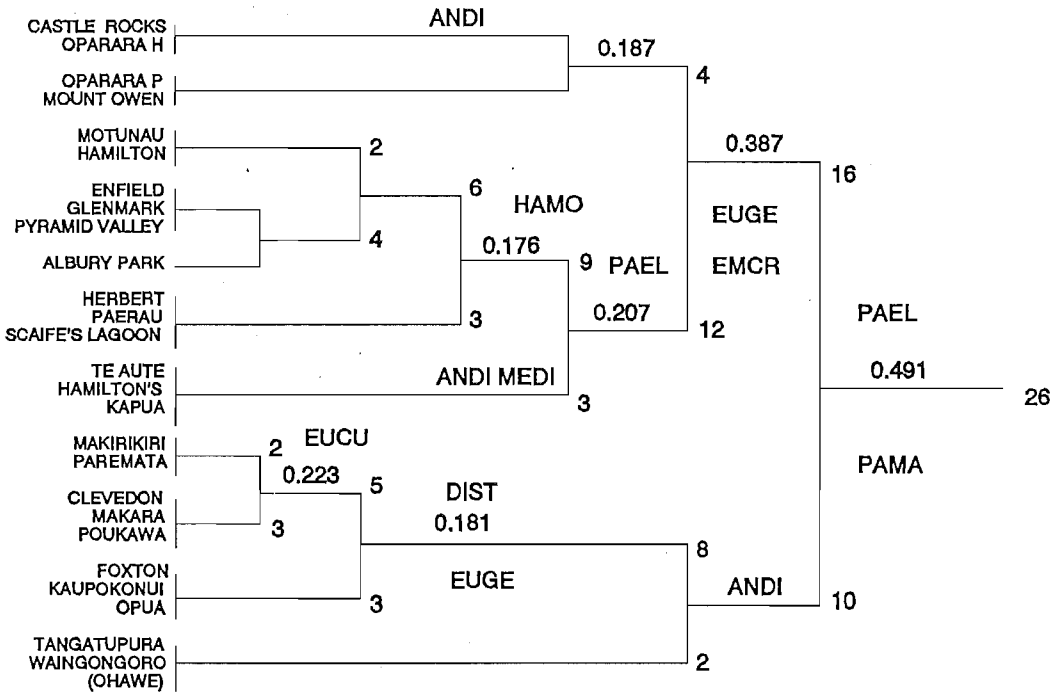

Fig. 9.6 Classification of sites using TWINSPAN on relative abundance data (Table 9.1B). Conventions as in Fig. 9.4, and in text.

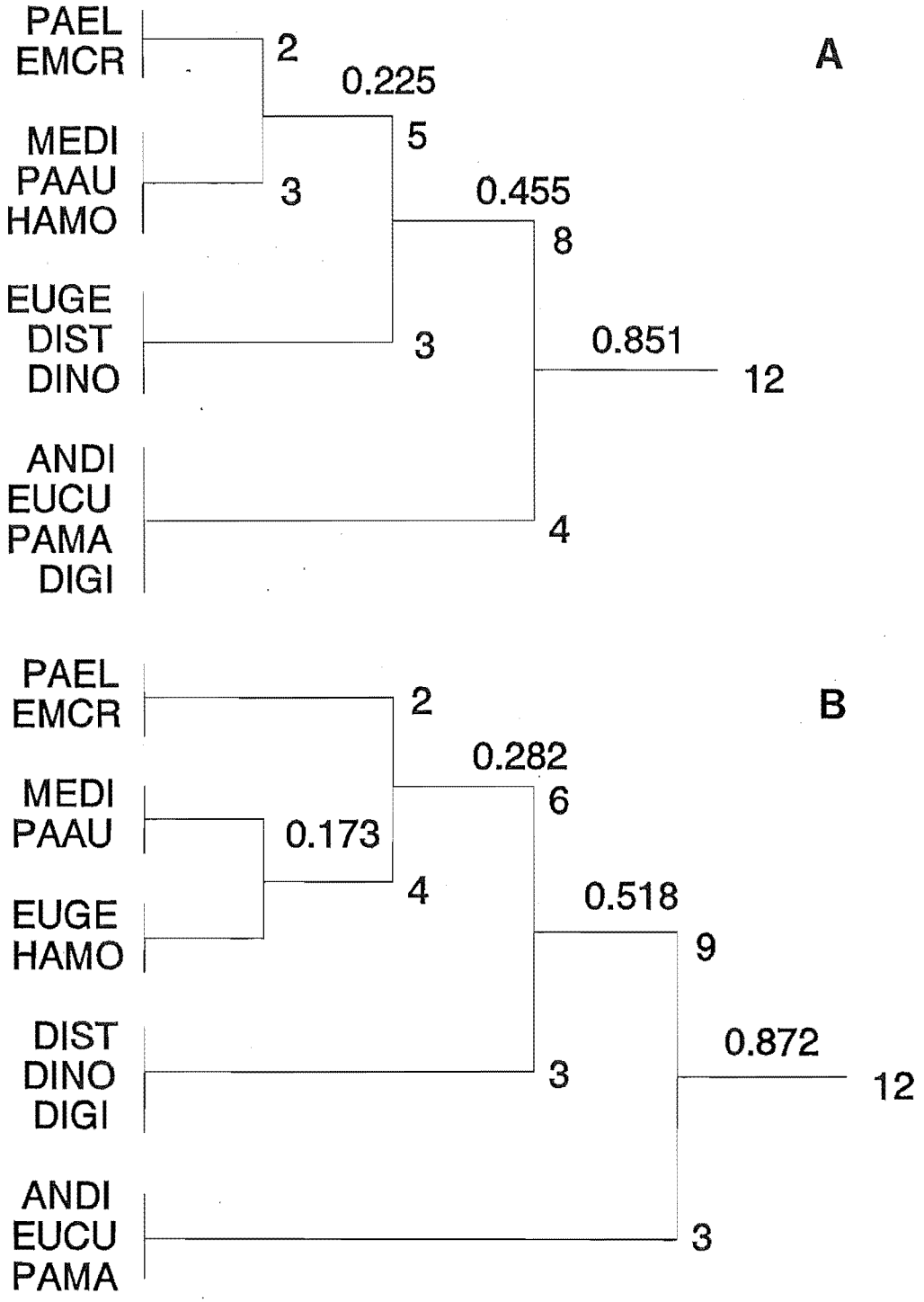

Fig. 9.7 A, B TWINSPAN classification of moa species plus Haast's Eagle: **A**, presence-absence data; **B**, relative abundance. See Table 9.3 for species acronyms.

Megalapteryx didinus (MEDI) and *Pachyornis australis* (PAAU) were mostly in the high country or far south, and *Euryapteryx geranoides* (EUGE) and *Harpagornis moorei* were commonest in eastern South Island sites.

DECORANA

Sites

Relative abundance (Fig. 9.8). High loadings on axis 1 indicated the presence of taxa from high altitude sites, or Pleistocene sites, which resembled present high altitude sites in their temperature range and vegetation. Low loadings indicated the dominance of lower altitude taxa. Axis 2 appeared to be strongly associated with taxon replacement along latitudinal gradients, with ecological factors affecting the exact loading of each site.

The third axis indicated the level of dominance of dinornithids at sites. Higher loaded sites had fewer species or lower numbers of dinornithids. Pyramid Valley, where *Dinornis giganteus* (DIGI) comprised 33% of the known moa fauna, had the lowest score on axis 3.

Species

Relative abundance (Fig. 9.9) High loadings on axis 1 were associated with higher altitudes. Taxa commonest in coastal sites had the lowest loadings. Axis 2 appeared to represent a latitudinal trend, complicated by the presence of cosmopolitan species. North Island endemics *Euryapteryx curtus* (EUCU) and *Pachyornis mappini* (PAMA) had the highest loadings on this axis, South Island endemics were intermediate, and cosmopolitan taxa had the lowest loadings. There was a much greater spread of axis 2 loadings for taxa with low loadings on axis 1.

Axis 3 loadings plotted against axis 1 again reflected the occurrence of *Pachyornis australis* (PAAU) and *Megalapteryx didinus* (MEDI) at higher altitudes, as shown by their high loadings on axis 1. Third axis loadings were more difficult to interpret, but seemed to separate drier inland montane basin sites in Otago (high loadings) from coastal and mesic environments. *Harpagornis moorei* had a high loading on axis 1 and a low loading on axis 3, indicating a

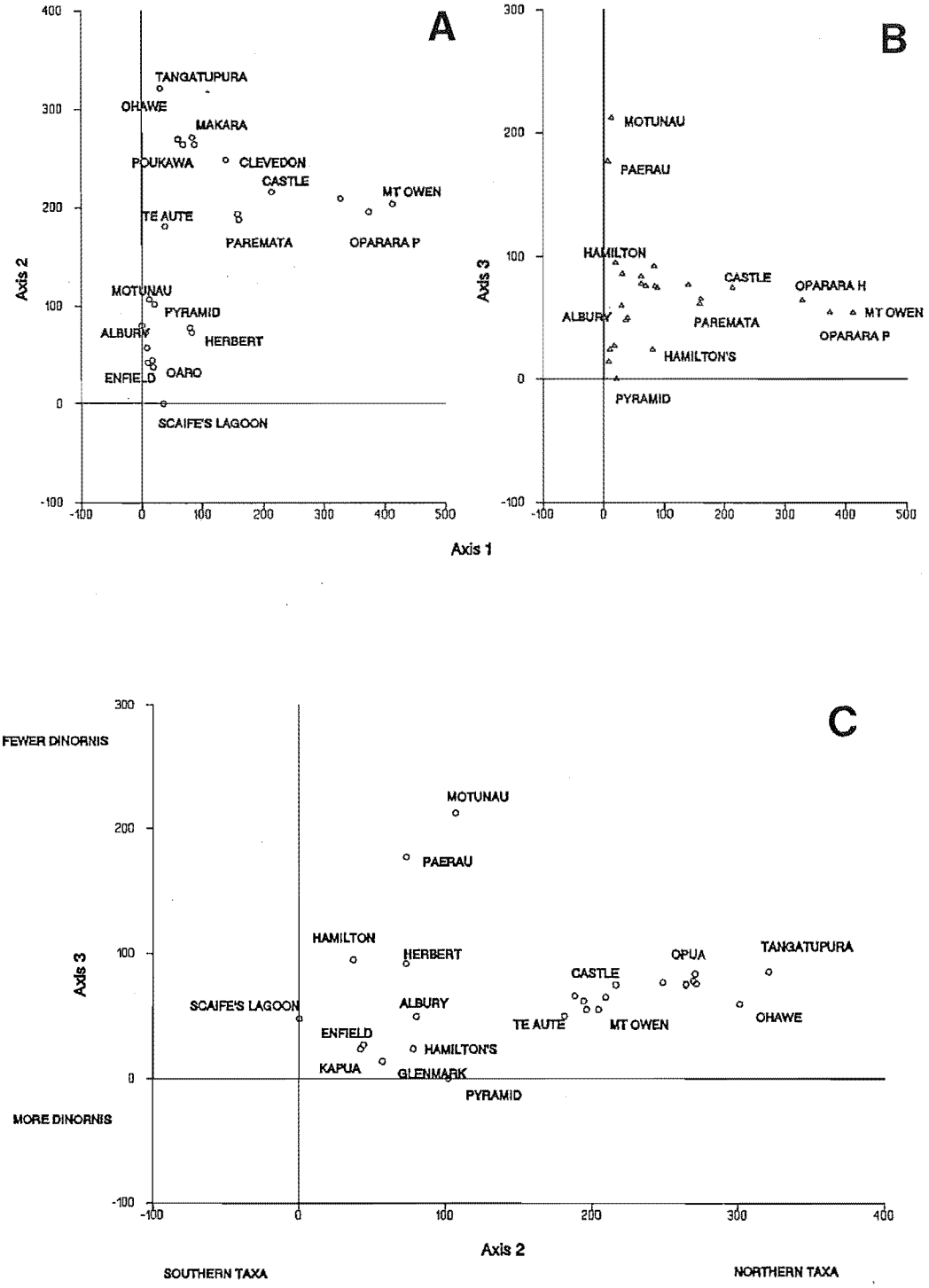

Fig. 9.8 (A-C) Position of sites on the first three axes of DECORANA ordination on relative abundance of moas and eagle: **A**, axis 2 v axis 1; **B**, axis 3 v axis 1; **C**, axis 3 v axis 2.

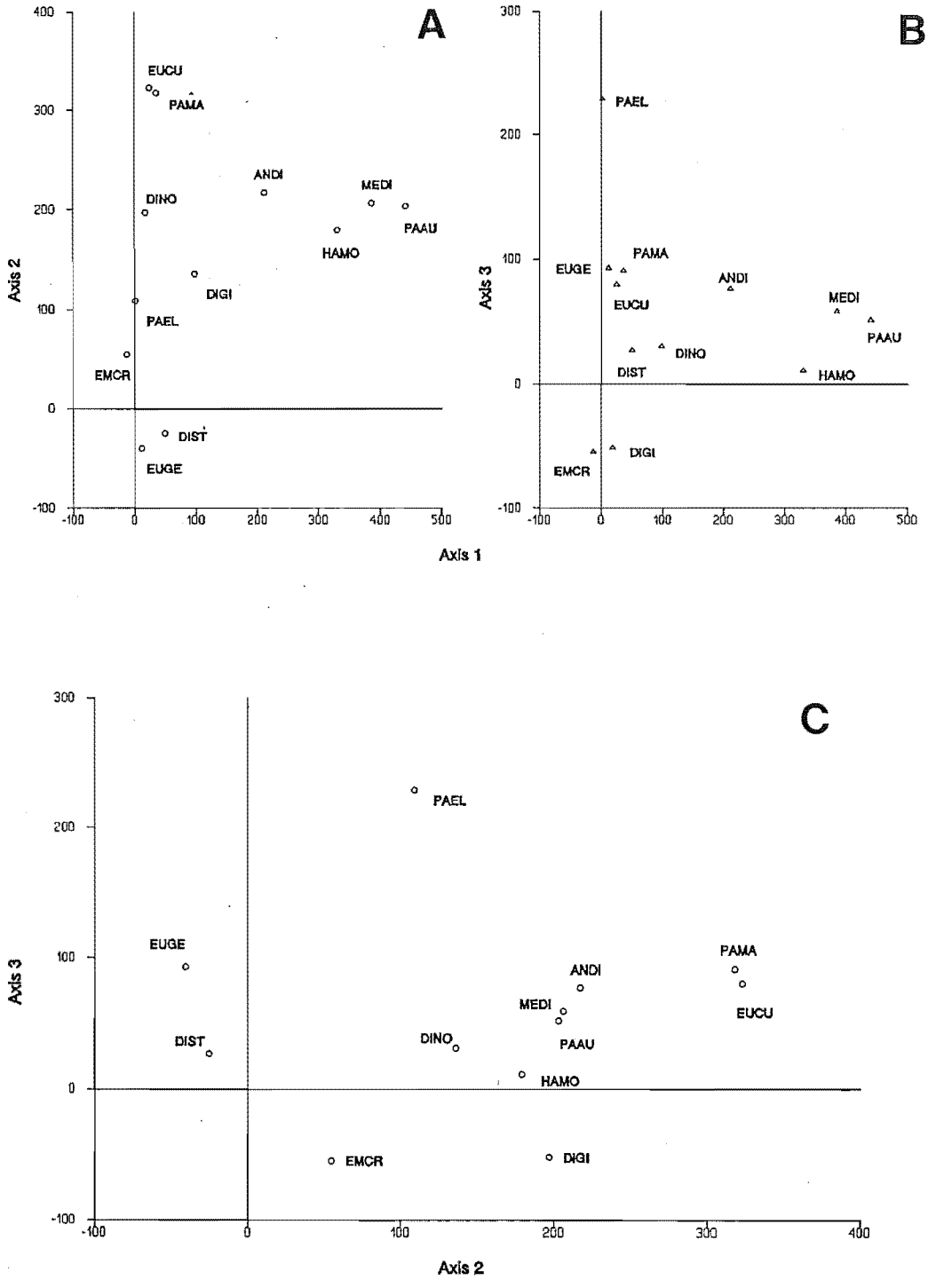

Fig. 9.9 (A-C) Position of moas and eagle on first three axes of DECORANA ordination on relative abundance of these taxa: **A**, axis 2 v axis 1; **B**, axis 3 v axis 1; **C**, axis 3 v axis 2.

tendency towards higher altitude and coastal habitats.

The plot of axis 3 against axis 2 placed *Harpagornis moorei* with a group including *Pachyornis australis* (PAAU), *Megalapteryx didinus* (MEDI), and *Anomalopteryx didiformis* (ANDI). The apparent proximity of these taxa to *Anomalopteryx didiformis* (ANDI) on the axis 2-axis 3 plot (where site effects were reduced) is misleading because *Anomalopteryx didiformis* had a lower loading on axis 1 and was well separated in 3-dimensional space.

9.3.4.3 11 moas, 26 sites

TWINSPAN

Sites

Relative abundance (Fig. 9.10A) The primary segregation was geographical, between northwest Nelson (3 sites) and the rest of the country. At the second division, the islands were separated mostly by island endemics, but Castle Rocks was included in the North Island suite because of the dominance of *Anomalopteryx didiformis* (ANDI). Te Aute appeared in the southern group because of the absence of North Island endemics (i.e. *Pachyornis mappini* (PAMA)) there during the Otiran.

Eastern South Island sites were distinguished by the dominance of *Emeus crassus* (EMCR) and *Pachyornis elephantopus* (PAEL) in one group, and *Dinornis novaezealandiae* (DINO) in the

other. The higher proportion of *Dinornis giganteus* (DIGI) separated Enfield and Kapua from Canterbury sites further north.

A mostly coastal North Island suite was indicated by *Euryapteryx curtus* (EUCU). One of two North Island sites lacking *Anomalopteryx didiformis* (ANDI) was Waingongoro (Ohawe), the only northern Holocene site with *Harpagornis moorei*. The remaining three North Island sites were inland or coastal backing onto hill country (Makara).

Species

Relative abundance (Fig. 9.10B) The species dendrogram constructed using moa abundances alone gave the best indication of possible species groups. The first

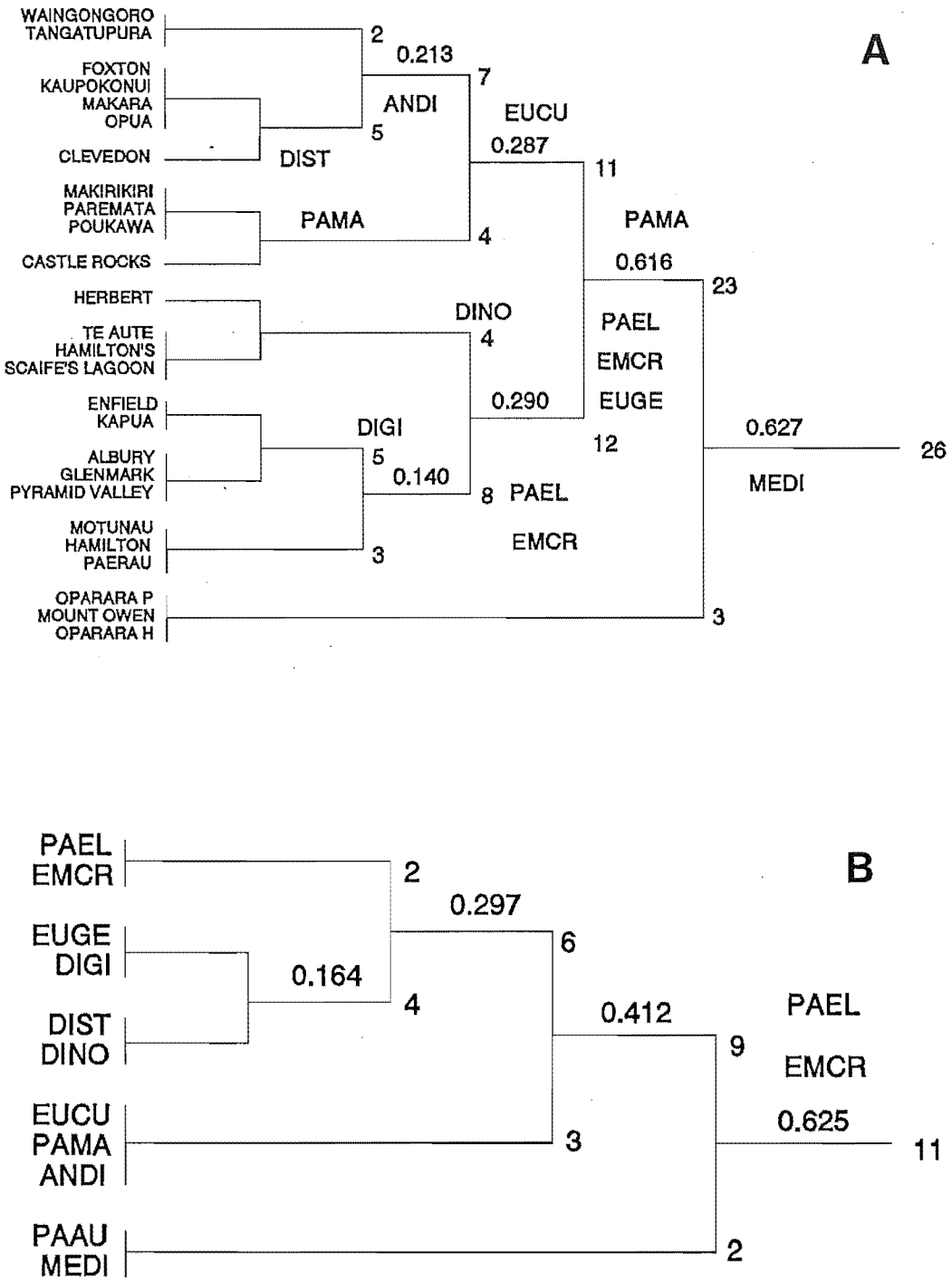

Fig. 9.10 (A, B) Classification of moas only using TWINSPAN of: **A**, sites; **B**, species. See Table 9.3 for species acronyms and text for other conventions.

division separated the pair *Pachyornis australis* (PAAU) and *Megalapteryx didinus* (MEDI) from all other species. On one branch from the second division, *Euryapteryx curtus* (EUCU) and *Pachyornis mappini* (PAMA) from the North Island were grouped with the cosmopolitan *Anomalopteryx didiformis* (ANDI). At the third division, the southern species *Pachyornis elephantopus* (PAEL) and *Emeus crassus* (EMCR) were grouped, as were the cosmopolitan dinornithids and *Euryapteryx geranoides* (EUGE). *Dinornis struthoides* (DIST) and *Dinornis novaezealandiae* (DINO) were then separated from *Euryapteryx geranoides* (EUGE) and *Dinornis giganteus* (DIGI).

DECORANA

Sites

Relative abundance (Fig. 9.11) Sites with high loadings on the first DECORANA axis were from higher altitudes or forested areas. Sites with lower loadings were closer to the coast or at least at lower altitudes. Axis 2 loadings indicated the relative dominance of dinornithids in the fauna (this factor was segregated along the third axis when Haast's Eagle was included). Lower axis 2 loadings echoed high percentage representation of dinornithids in a fauna.

Axis 3 appeared to represent a coastal (high) to inland (low) environmental gradient. Plotting axis 2 against axis 3 loadings clustered a few outlying sites with limited faunas.

Species

Relative abundance (Fig. 9.12) High loadings on axis 1 reflected higher altitudes, probably in combination with higher precipitation. The lowest loadings on axis 1 were for coastal or drier site taxa. Axis 2 loadings mirrored coastal to inland climatic gradients in the southern South Island, and loadings for inland, montane basin taxa were high.

If axis 2 indicates a precipitation gradient between sites, high loadings on axis 3 probably indicate a shrubland forest-scrub ecotone environment.

The apparently anomalous position of *Anomalopteryx didiformis* (ANDI) between *Megalapteryx didinus* (MEDI) and *Euryapteryx geranoides* (EUGE) was

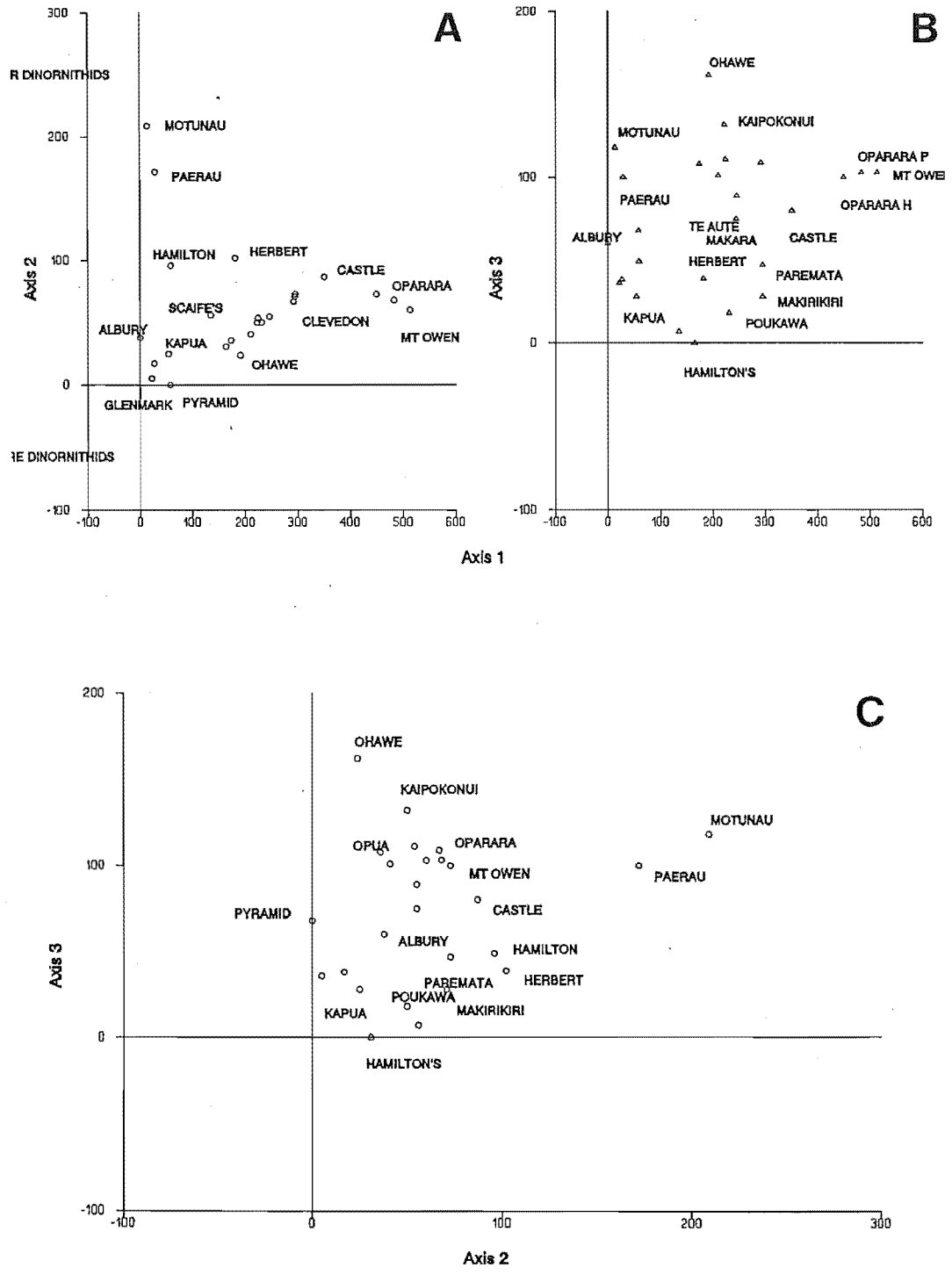

Fig. 9.11 (A-C) Position of sites on first three axes of DECORANA ordination, using abundance data for moas only: A, axis 2 v axis 1; B, axis 3 v axis 1; C, axis 3 v axis 2.

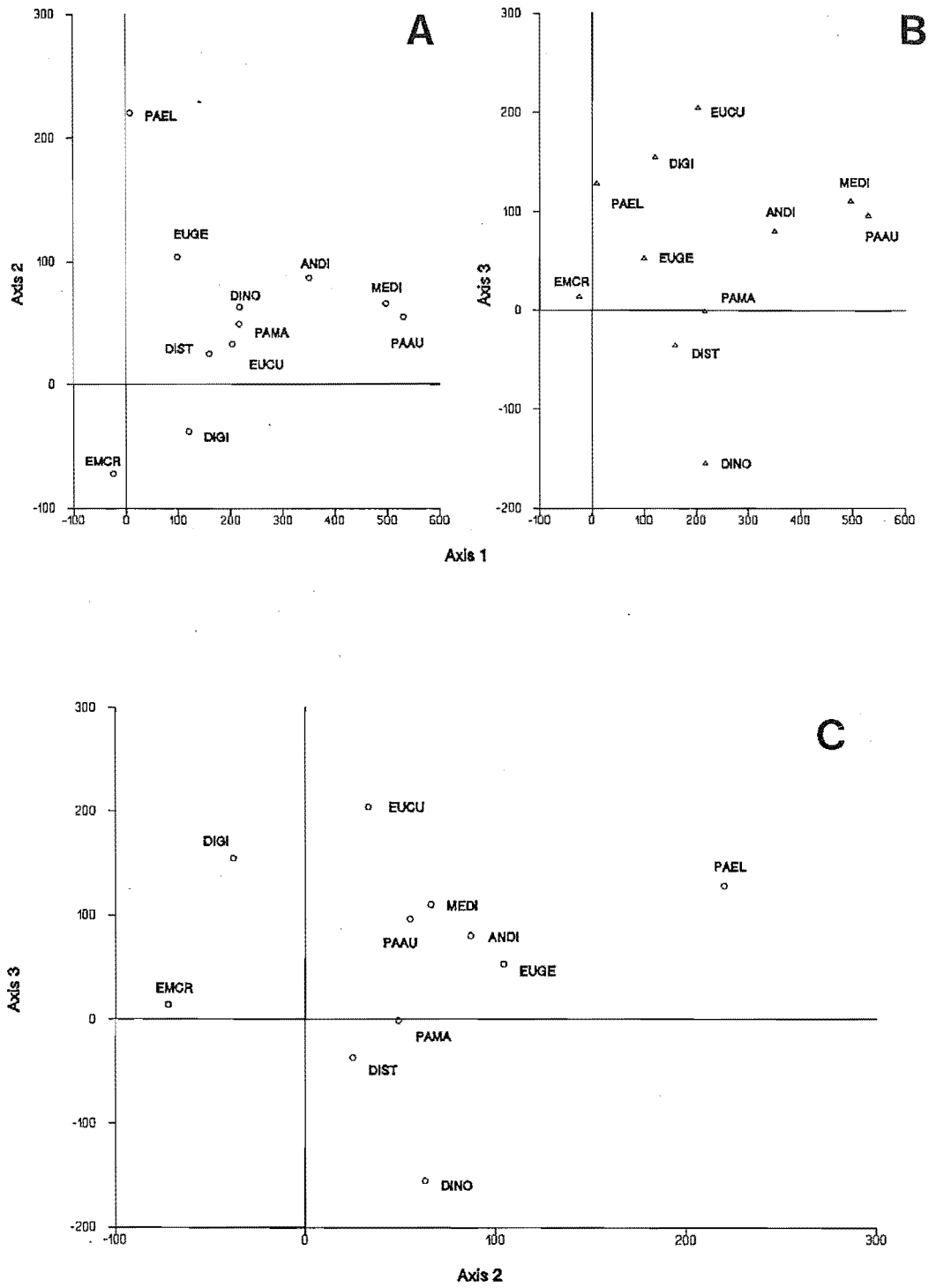

Fig. 9.12 (A-C) Position of moa species on first three axes of DECORANA ordination, using abundance data for moas only: **A**, axis 2 v axis 1; **B**, axis 3 v axis 1; **C**, axis 3 v axis 2.

resolved by its distance from these two along the precipitation gradient of axis 1.

The plot of axis 3 loadings on axis 1 showed that the moa taxa associated with *Harpagornis moorei* in the TWINSPAN analysis (*Megalapteryx didinus* (MEDI), *Pachyornis australis* (PAAU), *Euryapteryx geranoides* (EUGE)) were most abundant at forest-edge sites in drier areas, and extended into similar sites in montane areas. Taxa not associated with *Harpagornis moorei* (such as *Dinornis novaezealandiae* (DINO) and *Anomalopteryx didiformis* (ANDI)) were more typical of wetter, forested regions.

9.3.5 Moa habitat

Worthy (1990) presented maps of areas where each moa species reached local predominance. The results reported here were derived independently from a modified version of Worthy's (1990) samples, and are an independent test of his results. A species-by-species comparison (below) illustrates the level of agreement between the two approaches. The quoted passages are from Worthy (1990).

Anomalopteryx didiformis (ANDI) "Lowland, hill-country species, in podocarp forest". This species was closest on the DECORANA taxa plot of axes 2 and 3 to *Apteryx oweni* (APOW) and *Callaeas cinerea* (CACI), two species characteristic of lowland rain forest (Oliver 1955), and species which were, until recently, found in both main islands of New Zealand.

Megalapteryx didinus (MEDI) "Upland species, preferring relatively open habitat of upper montane forest, and very open herb and tussocklands of the subalpine zone". This South Island moa is second only to *Pachyornis australis* at the mountain end of the altitude axis; its nearest neighbours among living or recently extinct taxa are *Xenicus gilviventris* and *Traversia lyalli*, the first of which is now characteristic of subalpine scrub and rockfalls, and the second has been found from sea level to 1 600 m (Mount Owen, as a fossil, T H Worthy, pers. comm.). Allowing for its southern position on the latitudinal axis, its position places it in the upper forest zone.

Pachyornis mappini (PAMA) "Primarily lowland, probably preferring the

productive forest edge or shrubland ecotones provided by wetlands". As expected, this North Island moa is near the northern extreme of the latitudinal axis, between *Mohoua albicilla*, a North Island forest passerine, and *Apteryx australis*, which is also characteristic of wet forest (usually podocarp forest). It is also well towards the lower end of the altitudinal axis. *Pachyornis mappini* is next to *Cnemiornis gracilis*, which suggests that the northern flightless goose was also a forest bird.

Pachyornis elephantopus (PAEL) "Mainly eastern lowlands during the Holocene; in the West only during the Otiran". Worthy (1989) noted also that *Pachyornis elephantopus* "inhabited lowland forest margins or shrublands in dry areas": it is within the forest sector of the pattern, but near *Coturnix novaezealandiae* and *Gallirallus australis*, which suggests a forest edge or shrubland habitat. *Coturnix novaezealandiae* was also found in shrubland, in the downlands of Nelson and Canterbury.

Pachyornis australis (PAAU) "Mainly western and subalpine regions". A South Island endemic (Worthy 1989), this moa is at the extreme end of the altitude axis, suggesting a subalpine habitat. It is further along this axis than are *Nestor notabilis* and *Xenicus gilviventris*, which are both subalpine species (Falla *et al. 1979)*.

Emeus crassus (EMCR) "primarily a lowland eastern distribution in the South Island". This species is near *Anthus novaeseelandiae*. In the predominantly forested landscape of pre-human New Zealand (McGlone 1989), an association with *Anthus novaeseelandiae*, the pipit, suggests that the moa occupied a lake shore or forest-edge habitat, probably including riparian grasslands and shrubland.

Euryapteryx geranoides "New Zealand wide distribution in the lowlands, but a significant component of the avifauna only in eastern areas". This species is at the coastal edge of the forest domain. Its position between *Hemiphaga novaeseelandiae* (HENO) and *Gallirallus australis* (GAAU) on axis 2, and *Callaeas cinerea* (CACI) and a wetland-forest group on axis 3 suggests, however, that it preferred a more structurally diverse and drier habitat than that provided by lowland rain forest.

Euryapteryx curtus (EUCU) "a predominantly coastal distribution. Inland sites where it was numerous are probably all of glacial age except Holocene sites on the volcanic plateau". The DECORANA results suggest that this North Island species preferred lowland forest.

Dinornis struthoides (DIST) "a wide distribution over both islands, from lowland to subalpine areas; no correlation with particular altitude or rainfall zones". The smallest dinornithid is near mainly forest species on the axis 2-axis 3 plot, but is also close on the same axes to birds such as *Halcyon sancta* (kingfisher) of both open country and forest .

Dinornis novaezealandiae (DINO) "rare in coastal dune sites and in the eastern South Island; relatively common in the Holocene only in centre of the North Island and western districts of the South Island". This species was more closely associated with forest taxa than was *Dinornis struthoides*; it was remote from open country taxa on the DECORANA taxa plot.

Dinornis giganteus (DIGI) "Rare throughout the North Island; eastern lowlands in the South Island but even there was usually the rarest moa". The largest moa was grouped with a mixture of forest and wetland species, near the southern end of the latitudinal axis, as was expected from its abundance at Pyramid Valley.

9.4 DISCUSSION

Three major studies on habitat preferences of New Zealand's extinct birds have been published in the past decade (Anderson 1983, 1990; Worthy 1990). Although these have dealt mainly with one group of birds, the moas (Dinornithiformes), the results are relevant to other groups in the pre-human avifauna, because they have helped to clarify the range of environments available before human disturbance, and the general patterns of bird distribution.

The results reported in this chapter extend existing work by comparing the interrelationships of a wide range of species at many sites. The patterns of co-occurrence of living species found in the analysis of all taxa at all sites showed that clustering and ordination techniques could give biologically informative results. When site effects were removed, geographical and ecological patterns in the pre-human avifauna that matched present avifaunal patterns were revealed.

Cluster analysis was less useful than ordination for discerning ecological groups in the full fossil avifauna, but it did reveal clear regional site groupings. These effects seem to be based on differences in environmental and depositional regimes between regional faunas. Original site lists were independent, so any grouping of sites probably indicated real differences in community composition and distribution.

Presence-absence and relative abundance measures both gave useful results with both statistical techniques. However, as expected, relative abundance data allowed greater discrimination, particularly with TWINSPAN. Although presence-absence showed patterns in associations if enough samples were available, relative abundance was found to be better able to define factors affecting distributions. As several authors have pointed out (e.g., Anderson 1990; Caughley 1989; Flux 1989; Worthy 1990), it is not uncommon for a single site to contain examples of all moa species from one island. This has been taken as evidence that there was little ecological separation by habitat, and that size and bill shape were the main factors resulting in reduced competition for food (e.g., Atkinson & Greenwood 1989). The results presented here support Worthy's (1990) hypothesis that the emeid moas were separated ecologically by habitat as well as by diet.

9.4.1 DECORANA as a tool in fossil avifaunal analysis

The most important result of the first analysis was that the extant taxa represented at fossil sites were grouped by their known ecology and species distributions. Thus, DECORANA axis 2 and 3 loadings corresponded to ecological gradients between highland and coastal habitats, and between forests and wetlands, respectively. In addition, a latitudinal gradient indicating geographical replacement of species was evident. This pattern appeared even when many species of unknown ecology and habitat were included in the analysis, and it must therefore be assumed that the loadings revealed real differences in the habitat and ecology of extinct species too. If so, possible habitats should be discernible from the position of the fossil taxon relative to positions of extant species.

The pattern of geographical replacement of species is one way of checking the validity of this assumption. Not only were North and South Island taxa of moas, geese, and adzebills at opposite ends of the geographical axis, but so were the cosmopolitan taxa whose distributions were displaced according to their relative abundances.

My results indicate that most of the large extinct flightless birds were associated with extant forest taxa. However, groupings also suggest that the technique might discriminate between different types of forest and other habitats, if enough data on reliable indicator species were available. The separation of individual species from taxonomic groupings along non-geographical axes supports this interpretation.

For example, *Anomalopteryx didiformis* (ANDI) was associated with wet forest birds, whereas *Dinornis giganteus* (DIGI) was closer to species of wetlands and the coast. The two flightless geese (*Cnemiornis calcitrans* and *C. gracilis*) were amongst extant forest taxa, and were not especially close to other water birds. The small endemic duck, *Euryanas finschi*, was even further from the wetland pole, supporting suggestions that it was terrestrial and lived in open forest-scrub mosaics (Holdaway 1989; Worthy 1988).

Haast's Eagle was amongst birds whose habitat is forest margins, and near wetland species on the DECORANA plot; here it was near large flightless birds such as *Cnemiornis calcitrans* (CNCA), *Aptornis defossor* (APDE), *Emeus crassus* (EMCR), and *Pachyornis elephantopus* (PAEL). Its loadings on the second and third axes were identical to that of *Turnagra capensis*, a bird of forest and forest margins (Potts 1882), but it was far distant from that species on the first (site diversity) axis. The proximity to wetland species may be an artefact of its presence in swamp and dune sites. However, it was also near *Anthus novaeseelandiae*, which suggests forest margin, scrub or shrubland habitats.

The group containing Haast's Eagle was separated from lowland rain forest species such as *Philesturnus carunculatus*, *Strigops habroptilus*, and *Callaeas cinerea* by a group of birds, including *Coturnix novaezelandiae* and *Gallirallus australis*, of shrubland and forest margins. Haast's Eagle was separated from these taxa along the geographical diagonal axis, by its presence in more southern

sites rather than by its having different habitat preferences.

If Haast's Eagle had been further along the diagonal geographical axis, it would have been associated with *Euryapteryx geranoides, Dinornis struthoides*, and (if it had ranged into the far north) *Euryapteryx curtus*, *Aptornis otidiformis*, *Cnemiornis gracilis*, and *Pachyornis mappini*. Of these, *Euryapteryx geranoides* and *Dinornis struthoides* occurred in both islands, with *E. geranoides* being more common in the south (Worthy 1990). Its absence from areas where these were the dominant ground birds supports the view that the eagle was an active hunter taking a small range of preferred prey.

In general, the evidence indicates that Haast's Eagle had a restricted distribution in a widespread habitat (lowland forest and forest margins) despite the presence of apparently suitable prey in other areas.

9.4.2 Moas as typical eagle prey

I have already suggested that if Haast's Eagle was similar to other eagles it would have taken a range of prey up to the maximum size it could overpower. If it was an obligate carrion eater, the range of prey size would have been even larger because it could eat prey it had not killed. Large, carrion-eating birds are typical of habitats where large mammalian carnivores create a constant supply of carcases.

Unfortunately, the amount of other potential prey available to the eagle is unknown because data on the relative abundance of species are available for few sites, and the methods used in determining minimum numbers of individuals (MNI) have not always been stated explicitly. The largest and most homogeneous sample is that of Worthy (1990) for the moas.

I believe that the use of moas alone for a more detailed analysis of eagle-avifaunal associations was justified because moas constituted the most diverse group of potential prey for Haast's eagle. The various species replaced each other in deposits both geographically and chronologically, and the results of the broader analysis reinforce the notion that the Emeidae at least were separated by habitat as well as diet and size.

Worthy (1990) was the first to suggest habitats for individual moa species,

although Anderson (1983) presented strong evidence that the group of species living in central Otago during early Polynesian times were most common along watercourses in dense, mixed shrub associations.

Difficulties with moa taxonomy (e.g., Cracraft 1976) and with identification of individual bones have not helped the interpretation of moa distribution and habitat (Worthy 1987, 1989). However, some degree of stability of nomenclature has now been reached and sound bases for identification have been established (Worthy 1987, 1988, 1989). The emphasis is now on associating species with their particular habitats.

Anderson (1990) termed the two groupings of moas he recognised, the *Anomalopteryx* assemblage and the *Euryapteryx gravis* assemblage. The *Anomalopteryx* assemblage was typical of closed lowland forest, and the *Euryapteryx* assemblage species were more characteristic of open forest, scrubland, and forest edges (Anderson 1990). A clear association was found between the distribution of eagle sites and the distribution of the *Euryapteryx* assemblage.

This assemblage (after Worthy, as in Anderson (1990), except in not recognising *Euryapteryx gravis*) consisted of: *Euryapteryx geranoides; Euryapteryx curtus; Emeus crassus; Pachyornis mappini; Pachyornis elephantopus; Dinornis giganteus. E. curtus* and *P. mappini* were both North Island taxa, and *Dinornis giganteus* was present in both islands. The assemblage was widespread in the eastern and southern regions of the South Island and coastal areas of the North Island during the Holocene (Anderson 1990; Worthy 1990), and extended into the inland basins.

In the wetter lowland forests, species of the *Anomalopteryx* assemblage species (*Anomalopteryx didiformis, Dinornis struthoides* or *D. torosus*, and *D. novaezealandiae*) appear to have been more abundant. In subalpine scrub and fellfields at higher altitudes, and during the Otiran glaciation, *Pachyornis australis* also lived in more open habitats than members the *Anomalopteryx* assemblage. *P. australis* and *Megalapteryx didinus* seem to have formed the high altitude counterpart of the *Euryapteryx* assemblage, with *M. didinus* occupying both montane forests and fellfield.

As the comparisons above have shown, these associations were supported by my results. In addition, the TWINSPAN cluster analysis demonstrated a clear association between Haast's Eagle and three moas of the Emeidae. Using relative abundances, Haast's Eagle was most closely linked with *Euryapteryx geranoides*. As noted above, this species was common in the lowlands of the eastern South Island, where Haast's Eagle was apparently most abundant, but was rare in the North Island in the Holocene.

The other two moas were the higher altitude species pair of *Megalapteryx didinus* and *Pachyornis australis*. These apparently replaced *Euryapteryx geranoides* as potential prey for Haast's Eagle at higher altitudes. From Worthy's (1990) and my results, these were the moas most associated with more open, forest edge and shrubland or fellfield habitats.

Further south along the coast, and in the shrublands and forest edges of central Otago, *Emeus crassus* and *Pachyornis elephantopus* respectively, were added to the list of potential eagle prey.

The three dinornithids were not closely linked to Haast's Eagle in the TWINSPAN analysis, and may have been too uncommon (*Dinornis giganteus*), thinly distributed (*Dinornis struthoides*), or have occupied unsuitable habitats (*Dinornis novaezealandiae* to have been the eagle's usual prey.

All three moas of the remaining cluster appear to have been either birds of wet forest (*Anomalopteryx didiformis*), or widespread but rare (*Pachyornis mappini*), or confined to small areas of suitable habitat (*Euryapteryx curtus*). *Anomalopteryx didiformis* was the only moa species present at one site (Castle Rocks), but the site was not typical of the surrounding terrain or habitat.

9.4.3 Temporal changes

Anderson's (1990) associations seem to be valid temporally as well as spatially. Judging by the numbers of individuals represented, eagles were relatively abundant in the Oparara area between 21 000 and 10 500 years ago (Worthy & Mildenhall 1989). The pollen record for this period suggests that before 20 000 BP, the Oparara caves were in a forested valley floor, at the interface between subalpine and wet montane forests (Worthy & Mildenhall 1989). The bird fauna,

which included a range of extant forest passerine and parrot species, as well as the extinct gruiform *Aptornis*, the moas *Pachyornis australis* and *P. elephantopus*, and the quail (*Coturnix novaezelandiae*), remained unchanged until about 14 000 years BP. Worthy & Mildenhall (1989) suggested that open forests and shrublands were replaced by wetter lowland forests typical of the area today. Both moas of the *Euryapteryx* assemblage disappeared and *Anomalopteryx didiformis* appeared. By 11 000 years BP, *Aptornis* was absent and the fauna was typical of Holocene West Coast forests, with snipe (*Coenocorypha aucklandica*), and kakapo (*Strigops habroptilus*) present.

Cluster analysis of sites using abundance data supported this interpretation, at least for moa taxa and Haast's Eagle. The Holocene sites at Oparara clustered out with Castle Rocks, grouped on the presence of *Anomalopteryx didiformis* and the Otiran Oparara sites were linked with Mount Owen, where the two high altitude taxa were present.

When clustered without Haast's Eagle, the moas formed a slightly different pattern, apparently based on their ecology and geographic distribution. The *Pachyornis australis-Megalapteryx didinus* pairing was the most distinct. The major difference without the eagle was in the grouping of *Euryapteryx geranoides* with one of the dinornithids, the lowland *Dinornis giganteus*. This left the other two dinornithids together, and the other groupings the same as those with Haast's Eagle included.

The DECORANA analysis supported the same conclusions. Geographic and ecological replacement of taxa was demonstrated, and sites were grouped by species assemblage.

9.4.4 Prey availability hypothesis

The results supported the hypothesis that the distribution of Haast's Eagle was limited by the availability of suitable prey. There was a clear association with a limited number of moa taxa (EUGE, MEDI, PAAU), which replaced each other geographically and altitudinally. None of the four cosmopolitan moas was closely associated with Haast's Eagle.

The observed associations do not mean that these were the only, or perhaps even the major, prey taken by the eagle, as data on the relative abundance of other birds, such as the geese or adzebills is lacking. Geese and adzebills certainly occur at many eagle sites, as does the swan *Cygnus sumnerensis*. Some of these sites, such as the Glenmark peat lenses (Haast 1879), are of possible Oturian interglacial age. Such occurrences imply that eagles, geese, adzebills, and moas have been part of stable communities for long periods.

Apart from the other birds, the associations found in this study suggest that some moas were more susceptible to eagle predation than others. The taxa most closely linked with the eagle occupied more open habitats at the forest edge, and may have been more exposed to attack than species living in deep forest or thick scrub.

Alternatively, the richer food supply available in ecotone vegetation may have supported higher densities of these species. Most of the non-associated species clustered out with obligate forest birds; population densities were probably lower for forest taxa, as the difference in densities between cassowaries and emus noted by Anderson (1989) suggest. Size was apparently not a factor, because the non-associated groups contained both larger and smaller species than the associated ones (Atkinson & Greenwood 1989).

9.4.5 Obligate carrion hypothesis

My results do not support the hypothesis that Haast's Eagle was an obligate carrion eater. Its association with a small subset of species from the largest group of potential prey suggests that the preferred prey was not a random sample of the taxa available throughout the country, as would be expected if dead carcases were preferred to live prey.

In the pre-human environment, there would have been sufficient carcases of all sizes available at all times to support a substantial population of eagles. One of the largest eagles in the world, Steller's Sea Eagle (*Haliaeetus pelagicus*) subsists almost entirely on dead fish, seals, and whales, of which there would have been an abundance in pre-human New Zealand.

The pattern of moa distribution also suggests that the obligate carrion hypothesis is incorrect. Carrion sufficient to support small populations of eagles would have been available throughout the country. The eagle's apparent restriction to the eastern and southern parts of the South Island, open basins in the high country, and the southwestern coast of the North Island during the Holocene suggests that the type of prey was important, but that the environment was not. The kind of prey is likely to be important only if the eagle had to kill the prey before eating it. [Direct predation is strongly supported by bone damage on moa pelves consistent with claw marks of Haast's Eagle. These marks were found after this thesis was submitted.]

The rejection of the obligate carrion hypothesis does not imply that Haast's Eagle never ate carrion, but there is no direct evidence that it did so.

The hypothesis can also be refuted on ecomorphological grounds; this aspect is considered in Chapter 5.

9.4.6 Conclusions

The TWINSPAN and DECORANA analyses of fossil avifaunas revealed patterns that were interpretable by analogy with present-day faunal assemblages. Moas were the largest group of potential prey species for Haast's Eagle. The distribution of Haast's Eagle matched that of three emeid moas that had different habitat requirements. The distribution did not match that of the dinornithids, or of emeid moas of wet forest habitats. Other large birds were also associated with Haast's Eagle, but there were insufficient data to justify further interpretation.

The data do not support an hypothesis that Haast's Eagle was an obligate scavenger or carrion feeder. However, the data do support a hypothesis that the eagle's distribution was limited by the availability of preferred prey species, which were *Euryapteryx geranoides, Megalapteryx didinus,* and *Pachyornis australis*. Other taxa that were less closely associated, but important in southern and central South Island areas were *Emeus crassus* and *Pachyornis elephantopus*. All these species lived in ecotonal habitats or open areas that supported either large populations, or highly visible and vulnerable prey.

CHAPTER 4A

Department of Zoology, University of Canterbury, Christchurch

NEW ZEALAND'S PRE-HUMAN AVIFAUNA AND ITS VULNERABILITY

Summary: In the past 1000 years New Zealand has experienced a major 'extinction event', losing 40-50% of the avifauna, at least 50% of the frog fauna, and unknown proportions of the lizard and invertebrate faunas. During this period, bird species became extinct at different times and rates depending on the particular aspects of their ecology and life history which made them vulnerable to habitat loss, hunting, predation, and competition for food resources. Three groups of species with different levels of vulnerability are recognised within this event:
Group I, 1000-1200 AD - species susceptible to initial impact of hunting by Polynesians and dogs, and predation and competition for food after an explosive irruption of kiore (*Rattus exulans*);
Group II, 1200-1780 AD - species more resilient but gradually reduced by Polynesian hunting and continuous clearance and fragmentation of habitat;
Group III, 1780-present - species susceptible to hunting with European weapons and predation by *Rattus norvegicus, R. rattus*, mustelids, cats, and to competition by mammalian herbivores, and destruction of wet forest and wetland habitat.
Climatic change is seen as a negligible influence relative to these major intrusions. Discussions of the pre-human avifauna have so far concentrated almost exclusively on moas (Aves: Dinornithidae, Anomalopterygidae), partly because information on the other extinct species is sparse. The ecology of 12 species in the pre-human avifauna is inferred from their anatomy, relationships to extant species, sub-fossil evidence of diets, and analogy with related forms elsewhere.

Keywords: New Zealand; avifauna; extinction event

Introduction

The New Zealand avifauna was, when Europeans arrived, only a battered remnant of the fauna of pre-human times, surviving in a much-altered environment. This remnant, supplemented by some late immigrants is, however, the fauna used in most biogeographic and faunistic analyses. Various lists of extinct New Zealand birds are available (e.g. Kinsky, 1970), tucked away as appendices where they attract little attention. Most lists are out of date, and do not provide information on ecology. They are easily overlooked.

It is important to consider the ecology of species lost between 900 and 1800 AD in more detail, because only then can the causes and results of their extinction be better assessed. Cassels (1984) pointed out general similarities between the species which went extinct, but the present paper is the first attempt to assign a general ecology to several extinct species and to discuss faunal assemblages. As such, it may provide a framework for future work on the palaeo-ecology of the pre-human fauna, and a firmer conceptual base for studies on the relative effects of moas, ungulates, and climate on the vegetation of New Zealand.

To reconstruct the ecology of extinct species in the pre-human avifauna, some of which are only distantly related to extant species, we need to consider functional clues in their anatomy, and information on their habitat, diet, and demography. Some information can be obtained from the extensive, if uneven, literature on avian subfossil deposits in New Zealand, but we need many more, detailed studies of sites and individual species.

Such studies as are available have concentrated on the ecology of moas, and their influence on the evolution of the New Zealand flora. Moas (Aves: Dinornithidae, Anomalopterygidae) were indeed impressive members of the diverse avifauna in pre-human New Zealand, but their effects on vegetation in the Late Holocene cannot be discussed without considering the palaeo-ecosystem as a whole. Other herbivores were present and the moas (themselves a much more diverse ecological group than is usually appreciated) were subject to the same pressures of predation and dispersion of food resources as other animals. Several of the papers in this volume treat the group as 'the moa' and assign 'it' mammal-like

characteristics. Others argue on very tenuous premises for, say, flocking behaviour, and then attempt to assess population size and grazing pressure. The results are not convincing. Although many authors have discussed the cause(s) of moa extinction (e.g. Fleming, 1953, 1962; Cumberland, 1962; Duff, 1964; Anderson, 1984; Cassels, 1984; Trotter and McCulloch, 1984), only a few aspects of moa ecology have been treated in detail (Hamel, 1979; Burrows *et al.*, 1981; Anderson, 1983). To understand the relationship between these large avian herbivores, the ecology of individual species and genera of moas must be studied more deeply, in the context of a complete avifauna: it is that avifauna which is discussed here.

Palaeo-environment

The pre-human avifauna was dominated by forest and wetland birds. Forests covered most of the land below tree-line (McGlone, this volume), but the forest fauna was radically different from that documented by Europen explorers 100-200 years ago. Subfossil remains from caves and other deposits suggest that, before the arrival of Polynesians about 1000 years ago, the fauna was rich and diverse.

Declines in relict populations of *Powelliphanta* snails (Mollusca: Paryphantidae) (Meads *et al.*, 1984) and the large wetas (Insecta: Stenopelmatidae) (Watt, 1975) suggest that prehistoric populations were almost certainly far greater in numbers and more continuous. The great reductions in range, and the clear correlation between presence of introduced predators and absence or extremely low numbers of large invertebrates, lizards, and tuatara, strongly suggest that extinctions have occurred and that many mainland populations are now truly relict (Crook, 1973; Whitaker, 1973; Campbell *et al.*, 1984). Many of the disjunct distributions in the lizard fauna (e.g. *Cyclodina*) are in areas which were not greatly affected by climatic changes or physical disruption during the Pleistocene (Towns *et al.*, 1985). Conversely, one of the extreme relicts is *Leiolopisma acrinasum* which presumably survived through the worst of the glaciations in Fiordland or subsequently recolonised the area within a few thousand years.

Leiopelmatid frogs were widespread on both islands. Today, *Leiopelma hamiltoni* is restricted to Stephens and Maud Islands in the Marlborough Sounds, but has been found in cave deposits as far south as Punakaiki, and at Waitomo and Hawkes Bay in the North Island (Worthy, 1987a). Worthy (1987a) describes 3 new species of *Leiopelma* from cave deposits, including a species much larger than *L. hamiltoni*. Frogs must have been a major feature of the fauna of the pre-human forest floor, judging by the abundant remains being found in caves whose entrances were once within forest.

A variety of skinks (Scincidae) and geckos (Gekkonidae) still occurs on the main islands of New Zealand, but they are far more conspicuous and abundant on islands without mammals, particularly rats. Before humans arrived, lizards were probably as abundant on the mainland as they are now on the islands (Whitaker, 1973). Subfossil lizard material, usually not identified to species, has been found in caves and other deposits in many mainland areas (e.g. Rich *et al.*, 1979). Worthy (1987b) reports *Cyclodina alani, C. macgregori, C. whitakeri* and *Hoplodactylus duvauceli* from widespread localities in the North Island.

The tuatara (*Sphenodon punctatus*) is now confined to offshore islands, and breeds successfully only on those lacking the kiore or Polynesian rat, *Rattus exulans* and other *Rattus* species (Crook, 1973). Yet, the subfossil distribution of tuatara includes most parts of both main islands (Bull and Whitaker, 1975; Cassels, 1984). Its previous distribution indicates that it was a widespread member of the ground fauna when Polynesians arrived.

The endemic bat *Mystacina tuberculata* has exploited an unusually diverse range of foods in the absence of mammalian competitors. Daniel (1979) reports that it feeds on the ground, foliage, and tree trunk, takes insects on the wing, and eats fruits and nectar. In some ways it was an analogue of shrews, honey possums, and other bat groups. It also builds its own galleries in fallen trees and occupies petrel burrows. Not much is known about the only other New Zealand species, *M. robusta,* and it may even be extinct (Hill and Daniel, 1985), but it used to be widespread and is frequent in cave deposits near Waitomo (T. Worthy, pers. comm.).

Remains of petrels are prominent in many cave and dune deposits throughout New Zealand. Where the deposits are inland, in hills still covered with heavy forest, they probably reflect former breeding colonies. A few mainland colonies persist in some areas (e.g. *Procellaria westlandica* at Punakaiki, *Puffinus huttoni* near Kaikoura) or at least have existed in European times *(Procellaria parkinsoni* and *Pterodroma inexpectata*). Some of the dune deposits may indicate former colonies rather than beach strandings (Millener, 1981). Mainland cave deposits contain some of the small prions (*Pachyptila* spp.) and various

Pterodroma petrels now confined to offshore islands. Indeed, some islands (e.g. South East Island in the Chathams) still have diverse faunal assemblages resembling those inferred for many areas of the mainland (especially in forested hill country) before Polynesian colonisation. For example, populations of various burrowing petrels, tuataras, lizards, and large invertebrates are found on Stephens I and the Poor Knights Is.

When the drier eastern regions of Canterbury and Hawke's Bay were cleared 500-1000 years ago, large areas of forest associations were lost completely. Well before Europeans arrived, the forest/scrub mosaic prevailing in both regions from c. 10,000-1000 BP (McGlone, 1983) had been replaced by tussock grasslands with isolated patches of scrub and forest. The effects of these vegetation changes on the fauna may have been catastrophic. Olson and James (1982a, b) proposed that the drier forests of Hawaii, which were removed during Polynesian settlement, were more diverse in structure than surviving wetter forests, and many of the endemic birds confined to them were exterminated when this habitat was destroyed. A similar situation could have prevailed in New Zealand, and the present forest types may not include all those existing at the time of the first human habitation. For

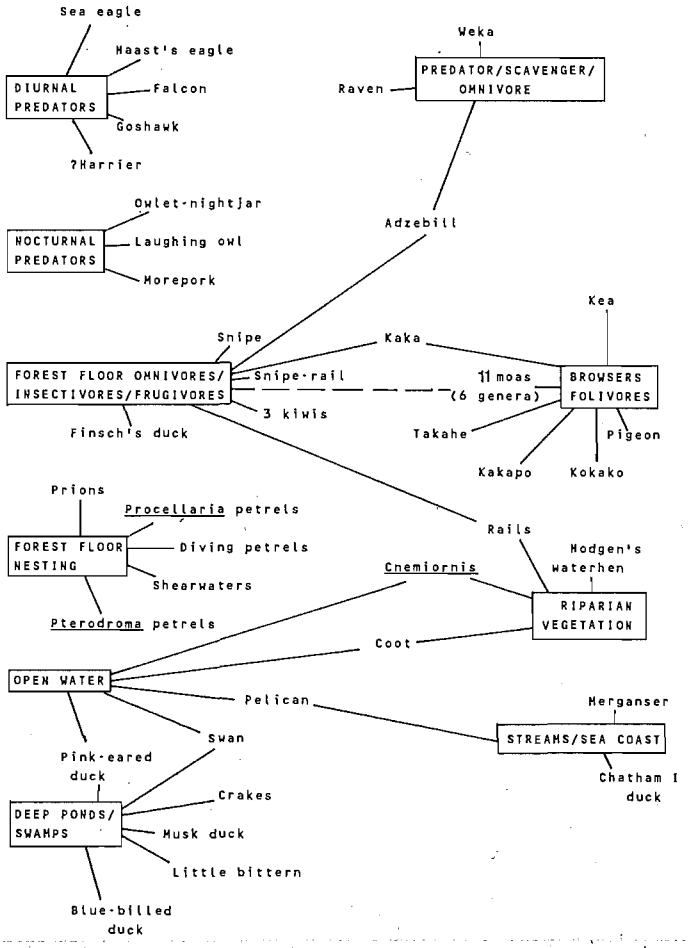

Figure 1: *Ecological and habitat groups in the pre-human avifauna of New Zealand. Each species is associated with its most likely habitat(s) or trophic strategy. Lines linking boxes indicate possible continua between categories, usually with the species linking them. Possible arrival after human colonisation indicated by ?*

example, I suggest that *Sophora* was more abundant in the forests over extensive areas in Canterbury and Otago; this would not be obvious in the pollen record because *Sophora* is pollinated by insects and birds. The lack of substantial amounts of trunk charcoal argues against *forests* of *Sophora* (McGlone, pers. comm.). Molloy (1971) illustrates some much-altered remnants of a *Sophora* association surviving on Great Island in the Rakaia River. McGlone (this volume) argues that *Phyllocladus alpinus/ Halocarpus bidwilli*-shrublands and *Podocarpus hallii*-hardwood forests were formerly widespread in dry areas, yet neither association has survived in quantity.

The pre-human avifauna

A systematic list of the genera of birds in the pre-human avifauna is given in Appendix 1. The avifauna can be divided into broad ecological groups (Fig. 1) which give some insight into the previous structure and composition of avian assemblages, and palaeo-habitat.

The loss of species through time is shown in Fig. 2. The shape of the curve from the arrival of Cook (1769 AD) to the present is based on published dates for last records and is, at present, the only part which can be drawn with any sort of precision. From its shape, I predict that the section of the curve for the first 10-50 years of occupation will also indicate an initial sudden loss of species (Group I) followed by extinctions of less vulnerable (Group II) species, and then those (Group III) which persisted as remnants into the European period or were vulnerable to further habitat destruction and the suite of predators introduced after 1769. After the immediate loss of several species when humans first arrived (circa AD 1000), the curve must, perforce, descend to the recent sudden decline commencing about AD 1800, but the exact shape will depend mainly on direct environmental influences. A steady decline over time (Curve A) implies a direct association between extinctions and loss of habitat. Conversely, a flattening in the curve followed by a steep section (or sections) (Curve B) could imply: restriction of many species to small refugia; more than one stage of habitat destruction; or that communities in different parts of the country were affected at different times.

The shape of the extinction curve therefore generates testable hypotheses about the cause(s) of the faunal collapse after 1000 BP. If it was a steady decline, as in A, then the various effects of human colonisation can be interpreted as having acted 'in concert' with species becoming extinct at random

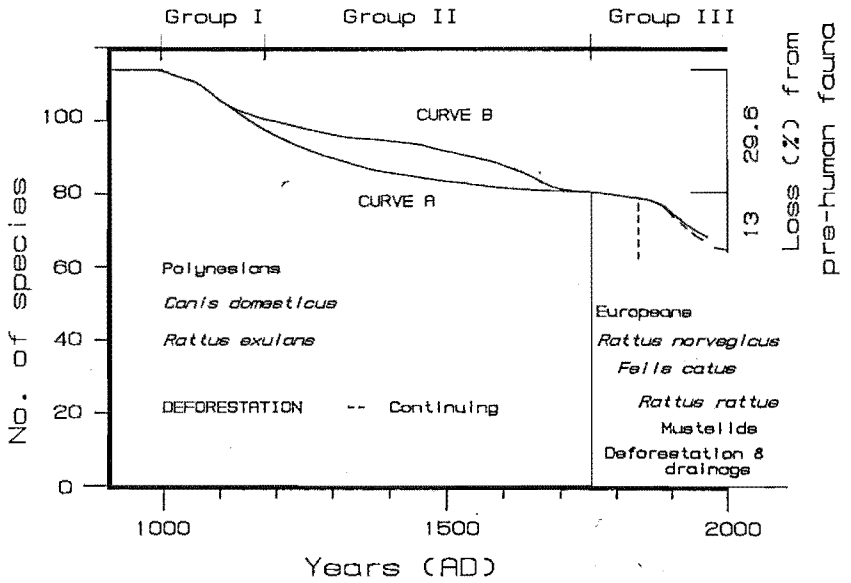

Figure 2: *Loss of bird species in South Island, New Zealand through time, since 900 AD. Percentage losses before and after European contact are shown at right. Groups I to III refer to species lost in each pulse of the extinction event (see text). Approximate dates for introductions of various species of mammal are shown. The shape of the extinction curves before European contact indicates two possible courses of species loss which can be related to changes in environmental conditions.*

intervals within the time span. If, however, as in B, the slope was not constant, the effects must have operated separately, or at the same rate but in different areas. The type of impact that contemporaneous environmental events may have had can be inferred from a knowledge of the ecology of the species lost in each pulse.

The Group I species would have included the pelican (*Pelecanus novaezealandiae*) which was probably extremely vulnerable to disturbance at nesting colonies (as is the Australian pelican *P. conspicillatus* (van Tets, in Frith, 1969)). Other Group I species were: the mainland race(s) of the snipe *Coenocorypha aucklandica*; the 'Stephens Island' wren *Traversia lyalli* (and two other acanthisittids which became extinct during the Polynesian period (Millener, 1988)); and *Capellirallus*, the 'snipe-rail'. All of these were potentially very vulnerable to predation by kiore (*R. exulans*). They were all small birds, structurally or behaviourally flightless, which lived and nested on or near the ground, and had no defences against mammalian predators. *Coenocorypha*, for example, now occurs only on rat- and cat-free islands. *Xenicus longipes variabilis* died out soon after an irruption of *Rattus rattus* on Big South Cape I, off Stewart I, in the 1960s (Merton, 1975).

At present, the impact of the kiore on the smaller birds may not be fully realised, but Crook (1973) and Atkinson (1978, 1985) indicate that populations of small vertebrates, including birds, can be greatly reduced by their predation on juveniles. Kiore probably spread rapidly from local centres of high populations which developed near the original landfalls, penetrating ahead of the human colonists, entering the dense forest, and reproducing exponentially in the presence of unlimited food. A rat 'blitzkrieg' (in the sense used by Mosimann and Martin (1977) for human predators in North America) may have advanced across the landscape; a grey tide, turning everything edible into rat protein as it went. The rat irruption may well be amenable to modelling using the Mosimann and Martin algorithm.

Whereas the avian predators were double-brooded at most, kiore could raise several litters in a season and some of those young could themselves breed in the same year. The principal characteristic of the prey fauna was not high absolute numbers but high diversity, as in a tropical forest today. The original equilibrium between predators and prey would have been upset easily and catastrophically by the arrival of a new, nocturnal predator with a high reproductive potential.

Those lost in a second pulse (Group II, e.g., most moas, the eagle *Harpagornis moorei*) probably succumbed through human hunting pressure, loss of habitat, and loss of food resources. For example, the declines in the moas, *Cnemiornis*, and swan would have been disastrous for the eagle population.

Group III species are those which were vulnerable to predation by Eurasian rats, cats, mustelids, and to habitat alteration by Europeans and introduced herbivores. It includes the shore plover (*'Thinornis' novaeseelandiae*), saddleback (*Philesturnus carunculatus*), and piopio (*Turnagra capensis*). Smith (1986) has shown that *Rattus rattus* is an efficient predator of nestling birds and invertebrates and that previous studies of rat diet may have underestimated the contribution of large invertebrates because rats select and consume soft flesh and thus have no identifiable hard parts in the gut. Preference for soft tissues also distorts stomach-sample estimates of predation on seeds by *R. exulans* (Campbell *et al.*, 1984).

Ecology and vulnerability

In the following list, New Zealand species have been assigned to Groups I or II on the basis of potential 'vulnerability', which predicts the period of extinction. These allocations and the hypotheses arising from possible shapes of the intermediate extinction curve can perhaps be tested when there are enough radio-isotope dates to refine the shape of that curve. Many moas have been dated but at present the only smaller bird dated directly by radio-carbon is *Euryanas finschi* at 1080 ± 70 yBP (NZ 4166) from Waikari, North Canterbury (McCulloch, 1977).

The 'field guide' style of entry is deliberate. Where possible, the information is based on general knowledge of ecology, life history, and vulnerability of related species in their own environment, extrapolated to the New Zealand situation. To give an overall picture of the species as parts of the *fauna*, I have included broader conjecture: there is much opportunity for further study.

Species list

Moa *Anomalopteryx, Megalapteryx, Euryapteryx, Emeus, Pachyornis, Dinornis*. Though treated here as one ecological group there was undoubtedly great diversity in ecology and life history within the family, and certainly between members of the currently recognised subfamilies, Dinornithinae and Anomalopteryginae. (Group II) Large to enormous

birds (25-250 kg). Larger species browsed on twigs, leaves, fruit; and also took fallen fruit from forest floor. Smaller species more omnivorous, diet including large invertebrates. Chicks of all species insectivorous, also taking small vertebrates. Adults adapted to low quality/high volume diet; monogastric digestion, with caecal microflora breaking down hemicelluloses (as in equids) and probably cellulose and lignin; material probably returned from caeca to at least small intestine and probably gizzard where microbial protein was broken down and absorbed. (cf. emus *(Dromaius novaehollandiae)* Herd and Dawson (1984)). Diet varied, so avoiding large doses of toxins from one plant species. Large trace element requirement. Diet changed to exploit vegetation of different heights during growth. Long-lived, 'K-selected'. Solitary, or small family groups. Nests usually under fallen tree or rock overhang; clutch 1-2; chicks creched in *Dinornis*. Most abundant in drier forest/scrub mosaic on younger, nutrient-rich soils, or on limestone; *Megalapteryx* penetrating alpine grasslands. Chicks taken by goshawk; chicks and adults of all species taken by Haast's eagle. Vulnerable to hunting by humans and dogs, habitat destruction, egg collecting, disturbance of traditional breeding areas, loss of food resources for chicks (large insects). Parallel with tuatara in that juvenile life history stage is most vulnerable - in tuatara from predation by rats, and in moas because rats consumed the food supply of the young.

Pelecanus novaezealandiae (New Zealand pelican) (Group I). Found on large lakes, rivers, and inshore waters. Food fish. Few large breeding colonies on low scrub or on the ground; very sensitive to disturbance at nest. North and South Is, both inland (Lake Waikaremoana, Lake Poukawa) and near the coast (Lake Grassmere). Hunted and disturbed at colonies by men and dogs; decline rapid because of lack of breeding success, killing of adults and removal of eggs.

Cnemiornis calcitrans (Flightless 'goose') (Group I). Large (10-15 kg, estimated from leg bone dimensions), flightless, terrestrial. Occurred in both islands. A grazer on short herbage like its presumed closest ecological counterpart, *Cereopsis novaehollandiae* (Cape Barren goose) of southern Australia; grazed herbs under open canopy and on riparian strips in forests. More abundant in the extensive areas of forest/scrub/grassland mosaic on drier eastern side of the South Island, inhabiting open seral forests of kanuka (*Kunzea ericoides*), seral grasslands, and the more extensive grasslands of Central Otago. Eggs and adults hunted by humans and dogs; eggs and chicks vulnerable to rats. Major areas of habitat destroyed. [*Cereopsis* survived only on islands off southern Australia and proved vulnerable to habitat destruction and predation. The various flightless geese of Hawaii did not survive the early period of human settlement (Olson and James, 1982b).]

Cygnus sumnerensis (New Zealand swan) (Group I) Throughout. Up to 3.5 kg. Food predominantly aquatic plants such as *Ruppia*, and terrestrial herbs obtained by grazing. Sensitive to disturbance and predation at large breeding colonies near lakes and lagoons. Eggs collected; adults hunted during annual moult.

Euryanas finschi (Finsch's duck) (Group I) Abundant throughout in forest and scrub. Flight poor. Food: invertebrates, fallen fruit. Nests built in cavities, under logs, or in cave entrances. Eggs and chicks vulnerable to rat predation. Rats competed for food. Much habitat lost with removal of drier eastern forests.

Oxyura sp. (Blue-billed duck) (Group I) Restricted to deep, permanent lakes and ponds with dense marginal vegetation, in breeding season: flocks on open water during moult. Food: small invertebrates, obtained by diving. Never abundant because of limited habitat. Vulnerable to rat predation on eggs.

Biziura delautori (New Zealand musk duck) (Group I) As for *Oxyura*; if anything, more vulnerable to predation on nests and adults.

Mergus australis (New Zealand merganser) (Group I) Found throughout. Nests on ground, among rocks or dense vegetation. Food small fish in lakes and rivers, and on sea coast. Vulnerable to rat predation on eggs and chicks; food supply and habitat not important factors in extinction because conditions similar to those on the Auckland Is (where it survived into this century) were still present on the mainland.

Pachyanas chathamica (Chatham Is duck) (Group I) Confined to Chatham Is. Marine: a 'steamer duck' analogue, feeding on molluscs and crustaceans obtained by diving. Nests in holes among rocks and in dense vegetation. Confiding, easily caught. Extinction through direct predation by humans.

Circus eylesi (New Zealand hawk) [This was referred to *Circus* by Scarlett in his original description; found to be a goshawk. A paper making the necessary nomenclatural change is in preparation, but because the ecology of the two raptor groups is so different, and the presence of a large bird hawk in New Zealand has been unrecognised previously, the bird is discussed here as a goshawk, in advance of the formal name change.] (Group II) Both main islands, in forest;

North I form larger. Weight 2.5-3 kg (female). Typical bird hawk, preying on species such as kaka (*Nestor meridionalis*), kea (*N. notabilis*), kakapo (*Strigops habroptilus*), pigeon (*Hemiphaga novaeseelandiae*), Finsch's duck (*Euryanas finschi*), weka (*Gallirallus australis*), kokako (*Callaeas cinerea*), and raven (*Corvus moriorum*). Much time spent perched on high branches; prey pursued in rapid, highly manoeuvrable flight through forest. Nest in large fork of tree, at 10-20 m; near water. Hunting range large. More abundant in drier forests east of main divides, and in areas of lower relief. Vulnerable to habitat destruction.

Haliaeetus australis (Southern sea eagle) (Group I) Chatham Is. Population small. On coast, feeding on fish, seal carrion, and marine birds (penguins and albatrosses). Highly vulnerable to disturbance at nest. Human predation on eggs and young most likely cause of extermination, although reduction of numbers of seals (by Polynesian hunters) and marine birds may have reduced food supply eventually.

Harpagornis moorei (Haast's eagle) (Group II) North and South Is. In forest, mainly east of the divide in the South I; not known north of Taupo. Immense forest eagle (male up to 10 kg, female up to 13 kg). Prey, large to very large ground birds, of up to 250 kg (e.g., *Cnemiornis, Aptornis, Megalapteryx, Euryapteryx, Pachyornis, Dinornis*). Prey taken by powerful strike after rapid descent from high perch. Long periods spent motionless; a 'sit-and-wait' predator. Carcase used for several days, bird(s) remaining in vicinity. Home range very large (15->30 km^2). Nest enormous, in emergent tree, used by same pair for many years. Life span 15+ years. One chick per pair, nestling stage protraced (100-120 days), dependent on parents for up to 1 year. Total population small. Vulnerable to habitat destruction, human predation at the nest, and ultimately to loss of large prey species.

Capellirallus karamu (Snipe-rail) (Group I) North I only, forest. Flightless, nest on ground. Weight 250-300 g. Food: invertebrates taken from soil and litter. Highly vulnerable to rat predation on eggs and chicks. Food source drastically reduced during initial rat plague. Same habitat as kiore. (cf. surviving banded rail (*Gallirallus philippensis*), now coastal in sedges and rushes.)

Fulica chathamensis (New Zealand giant coot) (Group II) Throughout, lakes, ponds, swamps, and along streams in forest. Weight 1.5-2 kg, cf. 500-1000 g for extant *F. atra*. Food, shoots and leaves of aquatic vegetation, seeds, and invertebrates for chicks. Susceptible to rat predation on eggs and young; dog and human predation on adults.

Gallinula hodgenorum (Hodgen's waterhen) (Group I) North and South Is, riparian swards, open forest glades, always near water. Weight 400-500 g. Food, shoots and stem bases of graminoids, seeds; food of chicks invertebrates. Short, grazed sward essential. Nest on ground, in tussock or clump of sedge. Vulnerable to rat predation of eggs and chicks. [*Gallinula mortierii* of Tasmania is a near relative; inhabits 'marsupial lawns' and, now, short grass pastures (Ridpath, 1964); extinct on mainland but widespread there in Holocene (Olson, 1975).]

Aptornis otidiformis (Adzebill) (Group I) North and South Is, forest. Flightless, 10-12kg. Food, large invertebrates, frogs, lizards, tuataras, petrels and petrel chicks; taken by turning over litter, tearing at rotting logs, and excavating burrows. Nest on ground, in heavy vegetation. Home range large. Vulnerable to hunting by humans, and to predation by feral dogs, rats (eggs and chicks), loss of habitat, and loss of food resources such as petrels and tuatara.

Megaegotheles novaezealandiae (Giant owlet-nightjar) (Group II) North and South Is, forest. Weight c. 200 g, cf. *Aegotheles*, 40-50 g. Flight weak, active on ground. Food large invertebrates, frogs, and lizards taken on ground. Nest in cavities and caves. Nocturnal. Vulnerable to rat predation, but more so to reduction of numbers and diversity of prey and perhaps loss of habitat. [May have survived into 19th Century (Potts, 1882).]

Corvus moriorum (New Zealand raven) (Group II) North, South, and Chatham Is; forest and scrub, usually near coast. Weight 900-1000 g. Omnivore, food including fruit, large insects, carrion (bird and marine mammal), lizards, tuatara, nesting petrels. Large stick nest in trees or on cliffs. Scavenger at *Harpagornis* kills. Possible predator on moa chicks. Vulnerable to human predation, habitat loss, reduction of food supply, particularly carrion.

Acanthisittidae (New Zealand wrens) (Group I/II) North, South, Stewart Is. Forest, scrub, subalpine scrub, throughout. Insectivorous, some fruit taken. Nests built in cavities domed, on or near ground in most species. Four species extant at European arrival, *Traversia lyalli* (and *Xenicus longipes*?) now extinct. *Traversia* widespread on mainland recently, *Xenicus gilviventris*, now confined to alpine and other rocky areas of South I, once (last glaciation?) found in North I (T. Worthy, pers. comm.). Two genera extinct by time of European arrival; one, at least, formerly widespread, abundant (Millener, 1988).

Extinct forms at least facultatively flightless ground birds. Vulnerable to predation by rats and cats, except *X. gilviventris* which lives in and on rock piles and in heavy scrub.

Discussion

In pre-human New Zealand, the avifauna was part of a much more diverse and abundant fauna than exists today. Whole assemblages of animals have since been lost, and probably some plant assemblages as well. The extinction event in New Zealand is one of the last faunal collapses of Holocene time and is equivalent to those in Madagascar and Hawaii (Olson and James, 1982a, 1982b). It has occupied about 1000 years which is about the same length of time as it took to lose the North American megafauna (Martin and Klein, 1984). However, the New Zealand event was unlike that in North America because there were no 'pivotal megaherbivores', whose removal could result in environmental changes sufficient to precipitate the extinction of other species (Owen-Smith, 1987). In New Zealand, humans could directly affect the environment on a large scale, in a short time.

Several hypotheses on the causes of extinctions in the avifauna have been proposed, including genetic degradation (Oliver, 1949), habitat change caused by changing climate (Falla, 1955), and combinations of these (Williams, 1962). Genetic degradation is unlikely to have affected an entire fauna of diverse phylogenetic stocks. Most of the fauna survived through the great climatic fluctuations of the Pleistocene, and small relict populations of species such as the snipe (*Coenocorypha aucklandica*) and the merganser (*Mergus australis*) survived into European times on islands. Evidence for massive habitat degradation during Polynesian times is overwhelming (McGlone, 1983) and most extinctions can be dated with reasonable certainty to the period after human colonisation. Williams (1962) was wrong in assuming that "the changes in the past 160 years were greater and more sudden than those of the previous 1600 or so". The conclusion is inescapable that the extinctions resulted from the manifold effects of human colonisation (Fleming, 1953, 1962; Cumberland, 1962; Cassels, 1984).

In summarising the decline of species in the European period, Williams (1962) overlooked the possibility that different groups in the avifauna could be vulnerable to different environmental stresses. The view that all species react in the same way to habitat loss and mammalian predation is implicit in most of the literature on extinctions in New Zealand. Each species has, of course, its own 'Achilles heel', but groups of species can be discerned which have similar vulnerability to environmental disturbances. The most vulnerable species group had been exterminated by 1769 AD; and forms lost since then were those which had been able to cope with the environmental disturbances associated with Polynesian culture, but not those brought by Europeans. The present avifauna consists largely of the most resilient species, usually the most recent colonists from Australia and elsewhere.

Event structure

This view requires that the extinction event involved two or more 'pulses' as different groups of species became extinct at different times in response to different environmental stresses. By tracking the extinctions through time, the vulnerability of each species and group to various contemporary factors can be inferred. The first pulse coincided with the introduction of three mammalian predators; *Rattus exulans, Canis domesticus,* and humans. These arrived in a land in which the birds were not used to mammalian predation, and depended for food on a ground fauna which was itself highly susceptible to predation. The second extinction pulse involved birds which were less immediately affected by mammalian predators, but more vulnerable to habitat destruction. The fauna was already depauperate when Europeans arrived, but there was yet another pulse of extinctions under the onslaught of cats (*Felis catus*), two more rats (*R. norvegicus* and *R. rattus*), and mammalian herbivores (bovids, marsupials) and omnivores (*Sus*). The combined effects of habitat loss and predation would probably have driven some species, such as takahe (*Porphyrio mantelli*) and kakapo (*Strigops habroptilus*), to extinction even if Europeans had not arrived.

Until many more dates of last occurrence are available, the species comprising the groups associated with each extinction pulse can only be inferred. I suggest that Group I includes species vulnerable to predation by kiore (snipe, wrens, rails); large, meaty species of open habitats (swan, *Cnemiornis*); and those of the more open eastern forests (moas, adzebill, *Cnemiornis*) whose behaviour and generally low population densities made them particularly susceptible to human hunting.
Similarly, Group II includes species (e.g. moas) susceptible to continued human and dog predation, and gross loss of habitat, and those which depended

on the diminishing supply of large and small prey (the raptors, raven, and perhaps moa chicks).

Group III species — saddleback (*Philesturnus carunculatus*), kokako (*Callaeas cinerea*), piopio (*Turnagra capensis*), and bush wren (*Xenicus longipes*) — appear to have been susceptible to predation by the two Eurasian rats, cats, mustelids, and perhaps to competition from mammalian herbivores. Although the moas constituted a guild of terrestrial *browsers*, there were no terrestial grazers to compete with takahe as do cervids today (Mills and Mark, 1977), so takahe were vulnerable to competition as well as mammalian predation. Hunting pressure was probably responsible for their original decline. R.J. Rowe (pers. comm.) has suggested that Group III species lived in denser, wet forests, and were comparatively safe until the Polynesians, who were reluctant to enter dense forest, began to clear it in the later stages of occupation (e.g., Best, 1942; McGlone, 1983). When metal axes became available, the Polynesians cleared dense forest to cultivate potato (*Solanum tuberosum*) (McGlone, 1983). Later, Europeans cleared much of the *remaining* lowland forest for livestock farming and introduced new predators, and the extinction rate accelerated again.

The laughing owl (*Sceloglaux albifacies*) was also lost in European times, although its numbers had been declining before then, at least in the North Island (Williams and Harrison, 1972). Large beetles could have been important in its diet, and perhaps bats and small birds. The rats reported from castings in the 19th Century were a relatively new item in the diet. Bats were probably important before they too declined.

Predators and the avifauna

The laughing owl survived into the 20th Century, but three other avian predators had gone extinct before Europeans arrived. The absence of two of these from the present fauna has led to fundamental misconceptions about the environment under which the flightless birds of New Zealand evolved. Haast's eagle and the goshawk were the largest of their kinds anywhere in the world. With the falcon, they constituted a guild of predators capable of exploiting the whole size range of prey, from wrens to the largest moa. New Zealand's avifauna did *not* evolve in the absence of predators, but only in the absence of *mammalian* predators. There was ample selection pressure for traits such as cryptic colouration and nocturnal habits (kiwi (*Apteryx* spp.), kakapo, kea, and kaka).

For example, the kakapo, is a large, terrestrial herbivore which exploits higher quality parts of the plant, such as shoots and young leaves. It has a lek breeding system (Merton *et al.*, 1984) because preferred food plants are dispersed, and carrying capacity of the habitat limited. It was probably constrained to being a *nocturnal* lek species by predation from the goshawk. Lek birds elsewhere, such as grouse in North America, are diurnal, but they are exposed to mammalian predators at night as well as diurnal raptors. Kakapo were abundant in areas subjected to little predation pressure from dense human populations in 'Classic' Polynesian times (post 1600 AD) but they declined dramatically after nocturnal mammalian predators such as cats were introduced.

Faunistics and biogeography

There were gains as well as losses in the avifauna during the Polynesian period, as well as since Europeans arrived. New niches resulting from changes in vegetation during the Polynesian period allowed new species to colonise from Australia. Several species, such as the morepork (*Ninox novaeseelandiae*) and harrier (*Circus approximans*), are rare or absent in pre-human deposits. Others, such as the grey teal (*Anas gibberifrons*) have been assumed to be recent colonists, although their remains have been found in deposits dating from pre-Polynesian times. Still others (pied stilt *Himantopus leucocephalus*, black-backed gull *Larus dominicanus*) have increased in abundance since Europeans arrived. Clearly, not all the members of the present fauna have been here since at least the end of the last (Otiran) glaciation. That misconception has led to the use of *current* species lists in biogeographical studies. It is not surprising that the extinct species are ignored when the 1970 checklist relegates species known only as subfossils to an appendix (Kinsky, 1970).

The most frequent application of island biogeographic theory in New Zealand has been in reserve design (e.g., Hackwell, 1982; East and Williams, 1984). This use is now being questioned (Williams, 1984; Boecklen, 1986; Zimmerman and Bierregaard, 1986). Species-area relationships based on drastically altered and incomplete lists provide a poor basis for management decisions, and the ecology of a threatened species is perhaps a better measure of the suitability of a projected reserve. A knowledge of the environment and assemblage in which the species evolved is fundamental to any study of its ecology. Ecological and biogeographical studies of the common

species in the present avifaunas are not very useful bases for management of the endemic forms endangered now. Similarly, discussions on the comparative effects of moas, ungulates, and climate on the evolution of New Zealand vegetation must be based on an understanding of the palaeo-environment and the ecology of the species living at that time.

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Appendix 1: *Systematic list of genera of birds breeding in New Zealand, excluding Antarctica and the Kermadecs, before 900 AD, with losses pre- and post-European contact.*

	No.of genera	No. of species	Extant (%) 'Cook'	Extant (%) today
Dinornithiformes				
Dinornithidae	1/0/0	3	0 (0)	0 (0)
Dinornis		3	0	0
Anomalopterygidae	5/0/0	8	0 (0)	0 (0)
Anomalopteryx		1	0	0
Megalapteryx		1	0	0
Emeus		1	0	0
Pachyornis		3	0	0
Euryapteryx		2	0	0
TOTAL	6/0/0	11	0 (0)	0 (0)
Apterygiformes				
Apterygidae	1/1/1	3	3 (100)	3 (100)
Apteryx		3	3	3
TOTAL	1/1/1	3	3 (100)	3 (100)

Sphenisciformes					
Spheniscidae		3/3/3	6	6 (100)	6 (100)
Megadyptes			1	1	1
Eudyptula			1	1	1
Eudyptes			4	4	4
	TOTAL	3/3/3	6	6 (100)	6 (100)
Podicipediformes					
Podicipedidae		1/1/1	2	2 (100)	2 (100)
Podiceps			2	2	2
	TOTAL	1/1/1	2	2 (100)	2 (100)
Procellariiformes					
Diomedeidae		2/2/2	8	8 (100)	8 (100)
Diomedea			7	7	7
Phoebetria			1	1	1
Procellariidae		6/6/6	24	24 (100)	24 (100)
Macronectes			1	1	1
Daption			1	1	1
Pterodroma			8	8	8
Pachyptila			4	4	4
Procellaria			4	4	4
Puffinus			6	6	6
Hydrobatidae		3/3/3	3	3 (100)	3 (100)
Garrodia			1	1	1
Pelagodroma			1	1	1
Fregetta			1	1	1
Pelecanoididae		1/1/1	2	2 (100)	2 (100)
Pelecanoides			2	2	2
	TOTAL	12/12/12	37	37 (100)	37 (100)
Pelecaniformes					
Pelecanidae		1/0/0	1	0 (0)	0 (0)
Pelecanus			1	0	0
Sulidae		1/1/1	1	1 (100)	1 (100)
Sula			1	1	1
Phalacrocoracidae		3/3/3	6	6 (100)	6 (100)
Phalacrocorax			3	3	3
Leucocarbo			2	2	2
Stictocarbo			1	1	1
	TOTAL	5/4/4	8	7 (88)	7 (88)
Ciconiiformes					
Ardeidae		3/3/2	4	4 (100)	4 (100)
Egretta			2	2	2
Botaurus			1	1	1
Ixobrychus			1	1	0
	TOTAL	3/3/2	4	4 (100)	3 (75)
Anseriformes					
Anatidae		12/5/4	16	8 (50)	7 (44)
Cygnus			1	0	0
Cnemiornis			2	0	0
Tadorna			1	1	1
Anas			4	4	4
Hymenolaimus			1	1	1
Aythya			1	1	1
Euryanas			1	0	0
Pachyanas			1	0	0
Mergus			1	1	0
Malacorhynchus			1	0	0
Biziura			1	0	0
Oxyura			1	0	0
	TOTAL	12/5/4	16	8 (50)	7 (44)

Falconiformes					
Accipitridae		4/1/1	5	1 (20)	1 (20)
Circus			1	1	1
Harpagornis			1	0	0
Accipiter			2	0	0
Haliaeetus			1	0	0
Falconidae		1/1/1	1	1 (100)	1 (100)
Falco			1	1	1
	TOTAL	5/2/2	6	2 (33)	2 (33)
Galliformes					
Phasianidae		1/1/0	1	1 (100)	0 (0)
Coturnix			1	1	0
	TOTAL	1/1/0	1	1 (100)	0 (0)
Gruiformes					
Rallidae		8/4/4	12	8 (67)	7 (58)
Rallus			1	1	1
Gallirallus			3	3	2
Porzana			2	2	2
Porphyrio			2	2	2
Gallinula			1	0	0
Fulica			1	0	0
Capellirallus			1	0	0
Diaphorapteryx			1	0	0
Aptornithidae		1/0/0	1	0 (0)	0 (0)
Aptornis			1	0	0
	TOTAL	9/4/4	13	8 (62)	7 (54)
Charadriiformes					
Haematopodidae		1/1/1	3	3 (100)	3 (100)
Haematopus			3	3	3
Charadriidae		3/3/3	4	4 (100)	4 (100)
Charadrius			2	2	2
Thinornis			1	1	1
Anarhynchus			1	1	1
Scolopacidae		1/1/1	2	1 (50)	1 (50)
Coenocorypha			2	1	1
Recurvirostridae		1/1/1	2	2 (100)	2 (100)
Himantopus			2	2	2
Stercorariidae		1/1/1	1	1 (100)	1 (100)
Catharacta			1	1	1
Laridae		1/1/1	3	3 (100)	3 (100)
Larus			3	3	3
Sternidae		1/1/1	5	5 (100)	5 (100)
Sterna			5	5	5
	TOTAL	9/9/9	20	19 (95)	19 (95)
Columbiformes					
Columbidae		1/1/1	1	1 (100)	1 (100)
Hemiphaga			1	1	1
	TOTAL	1/1/1	1	1 (100)	1 (100)
Psittaciformes					
Cacatuidae		1/1/1	1	1 (100)	1 (100)
Strigops			1	1	1
Nestoridae		1/1/1	2	2 (100)	2 (100)
Nestor			2	2	2
Platycercidae		1/1/1	3	3 (100)	1 (100)
Cyanoramphus			3	3	3
	TOTAL	3/3/3	6	6 (100)	6 (100)

Cuculiformes					
Cuculidae		2/2/2	2	2 (100)	2 (100)
Chrysococcyx			1	1	1
Eudynamys			1	1	1
	TOTAL	2/2/2	2	2 (100)	2 (100)
Strigiformes					
Strigidae		2/2/1	2	2 (100)	1 (50)
Ninox			1	1	1
Sceloglaux			1	1	0
	TOTAL	2/2/1	2	2 (100)	1 (50)
Caprimulgiformes					
Aegothelidae		1/0/0	1	0 (0)	0 (0)
Megaegotheles			1	0	0
	TOTAL	1/0/0	1	0 (0)	0 (0)
Coraciiformes					
Alcedinidae		1/1/1	1	1 (100)	1 (100)
Halcyon			1	1	1
	TOTAL	1/1/1	1	1 (100)	1 (100)
Passeriformes					
Acanthisittidae		5/3/2	7	4 (57)	2 (29)
Acanthisitta			1	1	1
Xenicus			2	2	1
Traversia			1	1	0
Pachyplichas			2	0	0
N. gen. 1			1	0	0
Meliphagidae		3/3/3	3	3 (100)	3 (100)
Notiomystis			1	1	1
Anthornis			1	1	1
Prosthemadera			1	1	1
Acanthizidae		1/1/1	2	2 (100)	2 (100)
Gerygone			2	2	2
Eopsaltriidae		1/1/1	3	3 (100)	3 (100)
Petroica			3	3	3
Corvidae		7/6/4	10	9 (90)	6 (60)
Turnagra			2	2	0
Mohoua			3	3	3
Rhipidura			1	1	1
Corvus			1	0	0
Philesturnus			1	1	1
Heteralocha			1	1	0
Callaeas			1	1	1
Sylviidae		1/1/1	1	1 (100)	1 (100)
Megalurus			1	1	1
Ploceidae		1/1/1	1	1 (100)	1 (100)
Anthus			1	1	1
	TOTAL	19/16/13	27	23 (85)	18 (69)
GRAND TOTAL		97/69/65	168	132 (78)	124 (74)
(without seabirds)		82/54/50	125	89 (71)	81 (65)

Notes: *'No. of genera' is given as number in pre-human fauna/number at time of Captain Cook's first voyage/number in present fauna. Extant 'Cook' is the number of species in fauna at time of Cook's first voyage.*

2. Extinct: 6 families, 32 genera, 44 species. Evidence is lacking for early occurrence of Gerygone, Halcyon, *and* Porphyrio melanotus *(T. Worthy, pers. comm. They are treated here as having been present.*

3. Passerine classification is after Sibley and Ahlquist (1985) and Holdaway (1988).

CHAPTER 4B

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Changes in the diversity of New Zealand forest birds

R. N. HOLDAWAY
Department of Zoology
University of Canterbury
Private Bag, Christchurch 1, New Zealand

Abstract Shannon diversity indices for several subfossil assemblages of New Zealand birds are compared with estimates for living communities today. As expected, bird species diversity was higher in the pre-human environment, but it was also greater than that predicted from studies of living communities. Previous estimates of the number of terrestrial bird species in the pre-human avifauna are too low, and many of these were incorrectly interpreted as being open-country species. The pre-human fauna was deficient in open-country birds. A prediction based on biogeographic (species-area) theory that this deficiency in open-country species was filled by half the species of moa (Dinornithiformes) is not supported by palaeoecological evidence. The major fall in bird species diversity in New Zealand is linked to the type of forest removed in Polynesian times, as well as the area.

Keywords bird species diversity; Shannon Index; forest birds; extinction; habitat

INTRODUCTION

Compared with other land masses of equal size closer to continental land masses, New Zealand has relatively few species of terrestrial birds (Slud 1976). The present terrestrial avifauna consists of species which have survived the environmental changes of the past 1000 years, and about 25 introduced species. The indigenous terrestrial birds are mainly forest species, and several of these are rare or restricted to large forest areas and inshore or offshore islands. Most of the introduced species avoid dense, wet native forest, but some, such as the chaffinch (*Fringilla coelebs*), song thrush (*Turdus philomelos*), and European blackbird (*T. merula*), penetrate deep into native forest stands and are now part of the forest ecosystem. Various studies (e.g., Kikkawa 1966), have examined the relative abundance of forest species in the present fauna, and McLay (1974) estimated the diversity of forest birds within different forest types and suggested some consequences of further forest loss and modification.

Although there is general awareness that the present indigenous fauna is the remnant of a much larger fauna, there have been few attempts to quantify the changes in the avifauna, apart from listing the birds which have been extirpated on each island. McLay (1974) predicted the diversity of forest birds in pre-European New Zealand, but did not extend this to pre-human times, or have data to test his prediction.

Flux (1989) calculated the expected number of species in the original fauna, according to island biogeographic theory. From the expected number of species on a landmass of New Zealand's size (Slud 1976), and assuming an equilibrium between open-country and forest species, he suggested that several species of moa (Dinornithiformes) occupied open (i.e., non forest) habitats. There has been considerable controversy over moa habitat and the total number of species (e.g., Anderson 1990; Atkinson & Greenwood 1989; Caughley 1977; Duff 1956). Flux (1989) argued from species-area relationships for the whole avifauna that there were "a total of 8–12 species [of moas], evenly distributed between forest and open-country". This would mean that four to six species of moa were primarily open-country birds. The discussion depends on the definition of forest bird: Flux (1989) defined a forest bird as one which "relies on" forest, whereas I prefer the broader definition of birds which have stable, long-term, forest populations.

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Flux's interpretation of total number of species depends in part on the definition of a land bird, and he followed Slud (1976) in excluding all rails and waterfowl. The applicability of this definition to New Zealand and other island ecosystems is evaluated here.

Recent publications on subfossil bone deposits in New Zealand include enough data on the relative abundance of species to allow a preliminary test of McLay's (1974) prediction of forest bird diversity, extended to pre-human times, to be made. The recent expansion in knowledge of the temporal and geographic distribution of extinct species (e.g., Worthy 1987, 1989a), data on distribution and composition of vegetation in pre-human and pre-European times (McGlone 1980, 1983; Nicholls 1980), and more secure systematic treatment of the moas (Cracraft 1976; Millener 1982; Worthy 1987, 1988, 1989b; Anderson 1990) also enable Flux's predictions to be tested. This paper presents the results of an analysis of faunas from four sites, ranging in age from Otiran glacial at c. 20 000 yr B.P., to the midden deposits of an early Polynesian community (600–900 yr B.P.).

METHODS

Diversity

I calculated Shannon diversity indices ($H' = -\Sigma p_i.\log_e p_i$; $H_{max} = \log_e S$, and $J = H'/H_{max}$ where p_i is the proportion of the total number of individuals belonging to the i th species and S is number of species) for four fossil avifaunas, using published data on minimum numbers of individuals recorded. Three of the four sites: Poukawa, Washpool midden, and F1 cave are in the North Island; the fourth, Honeycomb Hill Cave System, is in the South Island. The deposits are mostly Holocene in age, but Layer 3 of the Graveyard deposit at Honeycomb Hill caves is Pleistocene (Worthy & Mildenhall 1989). The sites were chosen because of the completeness of published information on numbers of individuals, and because present information suggests that they were forested during the period(s) of deposition. Species lists for the sites are given in Table 1.

For the Honeycomb Hill cave (Oparara) and Poukawa sites, diversity indices were calculated for each stratigraphically distinct layer, or for the stratigraphic subdivision of the site used by each author (Poukawa). Graveyard Layers 1 and 2 from Oparara (Worthy & Mildenhall 1989) were pooled; indices were calculated for the pooled fauna and for the Eagle's Roost (Oparara) fauna, and for Graveyard Layers 1 and 2 (c. 14 000–10 000 yr B.P. plus surface Holocene material) and Eagle's Roost faunas (16 000 yr B.P.–present) pooled. Worthy & Mildenhall (1989) indicated that the faunas were both accumulating in the Holocene, and they are so close geographically that they were probably sampling the same life assemblage. However, different depositional regimes and greater representation of the late Holocene in Eagle's Roost have resulted in different species representations at these sites.

The calculated values for fossil faunas were compared with McLay's (1974) predicted value of H' for the pre-European avifauna (Fig. 1) by plotting them on his fig. 1. To examine the relationship between H' values for fossil and living assemblages, I plotted H' for native forest species from McLay (1974) against $\log_{10} S$, and calculated the regression line. Regressions for the pooled fossil assemblages, and for all assemblages, were also calculated (Fig. 2b). The lines were then replotted on normal axes (Fig. 2c, based on McLay's (1974) fig. 1).

The evenness (J) value for each fossil assemblage was compared with those from modern sites reported by McLay (his fig. 2). The Shannon index depends on two variables: the number of species, and their relative representation, in the sample. Evenness is a measure of the departure of the sample from the limiting situation where all species are equally represented, and was used here only to see if the fossil assemblages differed greatly from the living samples in the proportions of individual species represented.

Values of H' and H_{max} for fossil assemblages were plotted on fig. 4 of McLay (1974) to enable a comparison with living New Zealand forest bird assemblages, and with the predicted diversity before European settlement.

Species-area relationships and New Zealand forest birds

Only the South Island fauna was analysed. Four lists of forest bird species breeding on the South Island were prepared: 1, using Flux's (1989) lists (working back from number of species reported) for A.D. 1840; 2, Flux's list plus other birds present in A.D. 1840 which, although they can live in open habitats, also live in forest; 3, list 2, plus extinct species, which by analogy with living relatives elsewhere, inhabited forest; 4, list 3, plus moas.

The numbers of species in each of these lists were plotted on fig. 1 of Flux (1989). Flux's point for species number for the South Island in A.D. 1840

Table 1 Minimum numbers of individuals for forest bird species in fossil sites used in the analysis. Data for Waitomo from Worthy (1984); Poukawa from Horn (1983); Washpool from Leach (1979); and Oparara from Worthy & Mildenhall (1989).

	Site											
	Waitomo							Washpool	Oparara			
	F1b	F1c Layer			Poukawa Layer			midden	Graveyard Layer		Eagle's Roost	Eagle's Roost + Gyd 1/2
Species		2/4	8	r	1	2	3		1/2	3		
Anomalopteryx didiformis	7	7	1	3					2			2
Megalapteryx didinus									4	73	3	7
Euryapteryx curtus	1											
Euryapteryx geranoides	1				1			2				
Pachyornis mappini	1	3	1		5							
Pachyornis elephantopus										4		
Pachyornis australis										30		
Dinornis struthoides	2	1		1							1	1
Dinornis novaezealandiae		1	1	1						1		
Dinornis giganteus	1											
Apteryx australis	1	6	3	2						1}	3}	3}
Apteryx haasti										}	}	}
Apteryx oweni	2	8		1							1	1
Apteryx sp.	1	8										
Euryanas finschi		4	3	1	3	26	17		45	36	3	48
Cnemiornis septentrionalis			2	3								
Cnemiornis calcitrans											1	1
Gallirallus philippensis						1		1		1		
Gallirallus australis	7	51	6	2	43	133	76	3	5	9	14	19
Capellirallus karamu	1	1	1		8	41	22	3				
Gallinula hodgenorum						4	32	15	2	1	1	3
Porzana sp.						2	5	3				
Fulica chathamensis							8	4				
Porphyrio mantelli	3	22	6	1	2	44	26			4		
Aptornis otidiformis	2	2	2	1	1			2	19		2	
Coenocorypha aucklandica	1	2	1		3	2			1		4	5
Harpagornis moorei										5	2	2
Circus eylesi	2				2	13	12		1	1		1
Falco novaeseelandiae					2	9	4			2		
Ninox novaeseelandiae							2	1				
Sceloglaux albifacies	1					2	2		4	4		4
Nestor notabilis									34	17	1	35
Nestor meridionalis		1			6	39	18	4				
Strigops habroptilus	11	21	5	1	4	34	29	1		10	11	
Cyanoramphus novaezelandiae					6	9	6	}	2}	1}	8}	10}
Cyanoramphus auriceps					1	2	1	95}	}	}	}	}
Hemiphaga novaeseelandiae				3	8	28	16	12				
Aegotheles novaezealandiae									4	1	4	5
Halcyon sancta								1				
Acanthisitta chloris											21	21
Xenicus longipes		1	1								12	12
Xenicus gilviventris									1		35	36
Traversia lyalli									5		14	19
Pachyplichas jagmi	1	1										
Pachyplichas yaldwyni									1		36	37
Wren n. gen. n. sp.											1	1
Petroica australis								4	3	1	49	52
Petroica macrocephala											10	10
Prosthemadera novaeseelandiae					7	5	1	87	2			2

(*continued*)

Table 1 (*continued*)

Species	Site: Waitomo F1b	Waitomo F1c Layer 2/4	Waitomo F1c Layer 8 r	Poukawa Layer 1	Poukawa Layer 2	Poukawa Layer 3	Washpool midden	Oparara Graveyard Layer 1/2	Oparara Graveyard Layer 3	Oparara Eagle's Roost	Oparara Eagle's Roost + Gyd 1/2
Anthornis melanura							1			2	2
Rhipidura fuliginosa							1			2	2
Mohoua novaeseelandiae										5	5
Mohoua ochrocephala										6	6
Mohoua albicilla		1									
Gerygone igata										1	1
Callaeas cinerea	3	6	7 1	8	19	13	2	6	5	55	61
Philesturnus carunculatus		1		2	8	2	2	1		9	10
Heteralocha acutirostris							1				
Turnagra capensis							3	1			1
Corvus moriorum					9	3		3	5	1	4

Note: Horn (1983) noted that much of the moa material from Poukawa was unidentifiable, but included *Pachyornis mappini* and species of *Euryapteryx*.

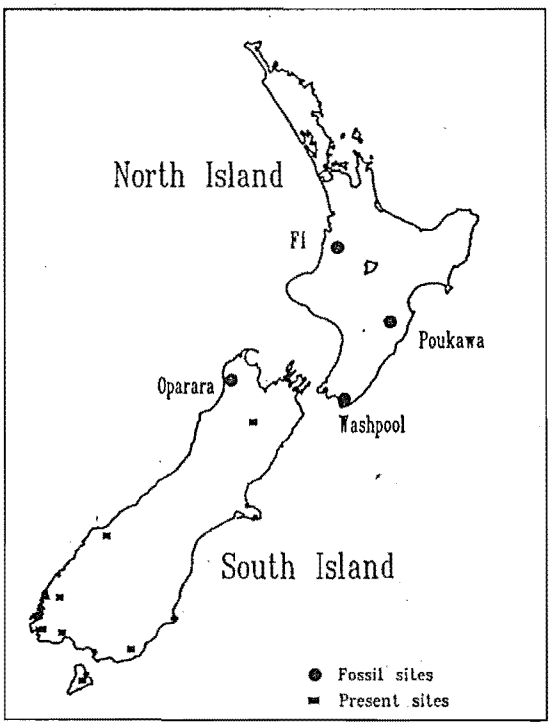

Fig. 1 Map of New Zealand showing location of major fossil sites referred to in this study, and general location of virgin forest sites used in McLay (1974).

was replotted using an estimate of South Island forest cover at European settlement based on McGlone (1989). This was done because Flux appears to have plotted the point at an estimate of forest area based on both islands, which grossly underrepresents the amount of forest lost from the South Island by 1840. The areas used here were 90% forest cover in pre-human period, reduced by 50% during Polynesian period, which gave a maximum forest cover at A.D. 1840 of 45% of land area. Most of that remaining in A.D. 1840 was high altitude beech forest or wet podocarp hardwood associations to the west of the main mountain ranges.

The curve (based on Arrhenius's power function) for species number against percent forest cover was replotted through the revised point (above). A curve using the species number from list 2 above at A.D. 1840 was also calculated, to pass through a corresponding point, also at 45% forest cover.

Species numbers from the four lists were plotted on fig. 2 of Flux (1989) for comparison with Flux's (1989) estimates of total number of land bird species, and number of "forest" and "open-country" species (Fig. 4).

RESULTS

Diversity

The values of H' calculated for the fossil assemblages were of the same order as those reported by McLay (1974) for present day assemblages including

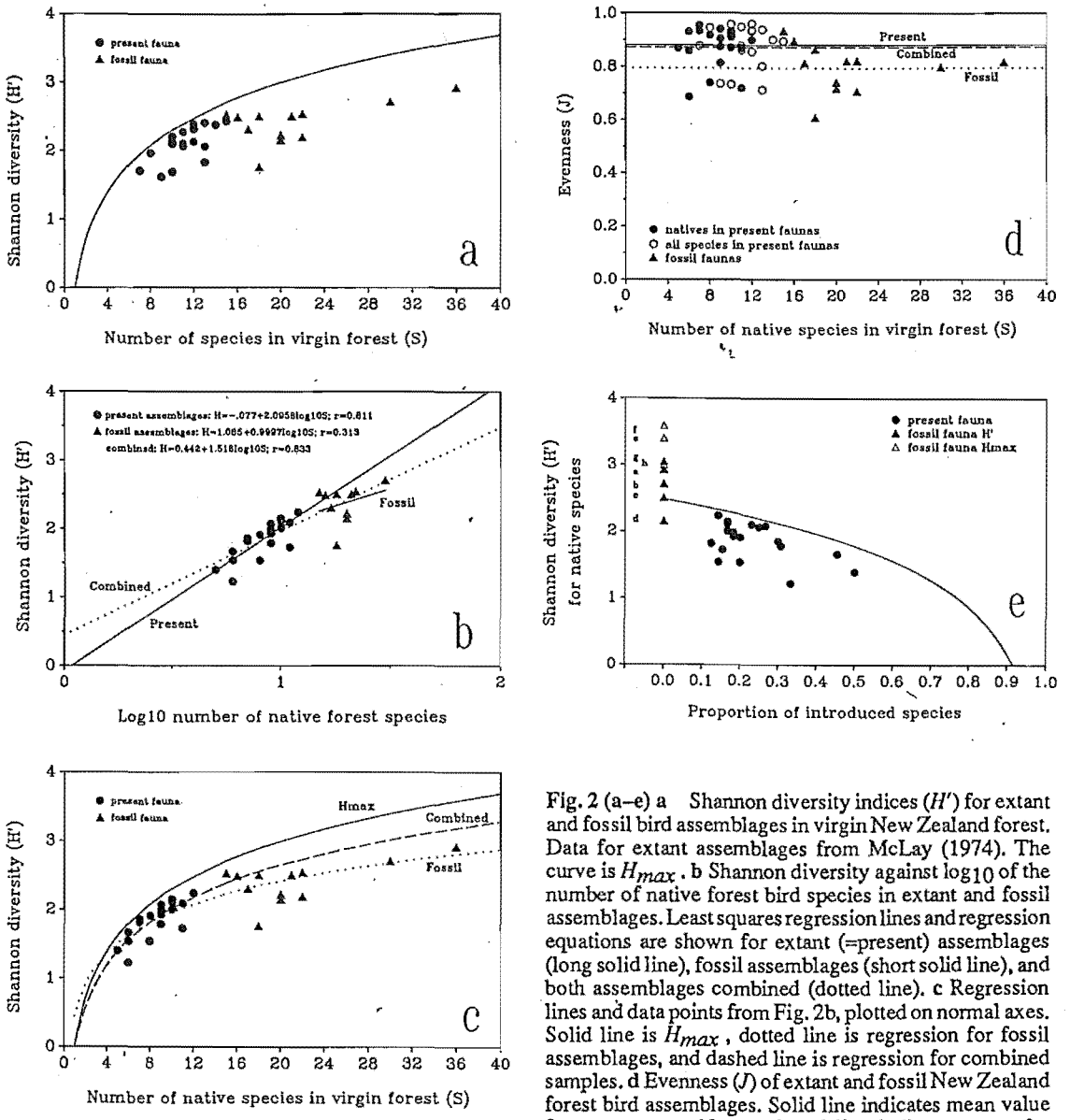

Fig. 2 (a–e) a Shannon diversity indices (H') for extant and fossil bird assemblages in virgin New Zealand forest. Data for extant assemblages from McLay (1974). The curve is H_{max}. b Shannon diversity against $\log_{10}$ of the number of native forest bird species in extant and fossil assemblages. Least squares regression lines and regression equations are shown for extant (=present) assemblages (long solid line), fossil assemblages (short solid line), and both assemblages combined (dotted line). c Regression lines and data points from Fig. 2b, plotted on normal axes. Solid line is H_{max}, dotted line is regression for fossil assemblages, and dashed line is regression for combined samples. d Evenness (J) of extant and fossil New Zealand forest bird assemblages. Solid line indicates mean value for extant assemblages, dotted line indicates mean for fossil assemblages, and dashed line the mean for all assemblages. e Prediction of diversity indices for pre-European bird assemblages. Points for present faunas from McLay (1974); curve is H_{max} for 12 native species in the present fauna, for increasing proportions of introduced species. Predicted value for pre-European is intercept of curve with y-axis (McLay 1974). Filled triangles are H' values for: a, Eagle's Roost + Graveyard L1+L2; b, Eagle's Roost; c, Poukawa L3; d, Graveyard L3. Open triangles are H_{max} values for: e, Eagle's Roost; f, Eagle's Roost + Graveyard L1+L2; g, Poukawa L3; h, Graveyard L3.

introduced species (Fig. 2a). Maximum diversity was obtained for the most "complete" fauna (Graveyard Layers 1 and 2 plus Eagle's Roost). The values of H' for present day native bird assemblages were highly correlated with the log of species number, ($H' = 0.077 + 2.0958.\log_{10}S$, $r = 0.811$; Fig. 2b).

H' values for fossil assemblages showed greater scatter, but the combined data sets also gave a highly significant correlation (Fig. 2b). H' values for all fossil assemblages were generally higher than for

present native bird faunas, but they decreased less rapidly with increasing H_{max} (Fig. 2c; solid line) than expected from the least squares line calculated from present faunas (Fig. 2c: broken line). The least squares regression for the fossil and present native faunas combined is shown by the dotted line in Fig. 2c.

Evenness (J) values for present and fossil faunas were very similar (Fig. 2d).

Figure 4 of McLay (1974) is reproduced here as Fig. 2e, with H_{max} and H' values for fossil assemblages plotted as well. The predicted value for the pre-European fauna (2.5 = 12 equally abundant native species with no introduced species; see Fig. 2c) is shown by the intercept of the solid line with the y-axis. All fossil H_{max} values, and two of the H' values were greater than this value. H' for Poukawa 3 (with few small passerines and less deposition time than Poukawa 1 or 2) was at the intercept and only the Otiran fauna at Oparara was smaller.

Species-area relationships

Forest species

The species lists used for the biogeographic analysis are shown in Table 2 and were compiled as follows:

List 1. The 27 forest birds known to be present in the South Island in 1840 are given in the first column of Table 2. Flux (1989) accepted 27 species but did not list them. He in fact included the laughing owl (*Sceloglaux albifacies*) instead of the the falcon (*Falco novaeseelandiae*) (J. Flux, pers. comm. 1990). *Cyanoramphus malherbi*, which is included in the 1970 checklist (Kinsky 1970), is assumed to be a valid species.

List 2. To the 27 species listed in Table 2 are added the kea (*Nestor notabilis*), the kingfisher (*Halcyon sancta*), and the laughing owl (*Sceloglaux albifacies*). The differences between lists 1 and 2 are not critical, nor is the possible exclusion of *Cyanoramphus malherbi*. That Flux (1989) accepted *Sceloglaux albifacies* and rejected *Falco novaeseelandiae* (which does not "rely on" forest although it is a well known inhabitant of North Island and West Coast forests (Fox 1978)) is irrelevant to the totals. The higher total (30) including *C. malherbi* is accepted here.

The arguments developed here and in Flux (1989) depend heavily on which species are considered to be forest birds, so some justification for including the three species is desirable.

O'Donnell & Dilks (1986) reported the kea in West Coast forests from lowland forest (rarely) and from the valley floor to the bushline in high country valleys. They were observed in several forest types, including rata, kamahi, and silver beech.

Despite Oliver's (1955) comment that the kingfisher "is more of a bird of the open than of the forest", kingfishers are conspicuous residents of many forest areas, usually near the edge, and along streams, but also "well into forest" (O'Donnell & Dilks 1986). O'Donnell (1981) reported that the foods of kingfishers from three sites included many forest insects. Robertson et al. (1983) included it in a discussion of forest birds from the southern North Island.

Williams & Harrison (1972) suggested that the laughing owl was a bird of rocky areas and the forest edge, but it has been recorded from forested areas of both the North and South islands. Subfossil remains have been found at sites such as Pyramid Valley (Scarlett 1955) where it was associated with a forest avifauna, and where forest was the dominant vegetation at the time of deposition (Burrows 1989). Williams & Harrison (1972) advocated a grassland habitat on the basis of the best-documented records from last century, those of T. H. Potts and W. W. Smith in inland and South Canterbury. In these areas, the birds were associated with rocky ground, and forest remnants.

I suspect that the laughing owl was primarily a forest species and that the abundance of records from grassland areas reflects both the presence of acute observers in those areas, and the ease of observation in forest edge or open habitats. The rocky hillsides of South Canterbury had patches of forest and, as suggested by Williams & Harrison (1972), the fur reported from owl castings was as likely to have been from native bats as from the introduced kiore (*Rattus exulans*). The long-tailed bat (*Chalinolobus tuberculatus*) is still found in the area (Daniel & Williams 1984). In any event, kiore do live in forest.

Plausible arguments can be presented for including other birds, especially the brown teal (*Anas aucklandica*), in this list. Williams (1964) suggests that this duck was originally characteristic of swamp forests of kahikatea (*Dacrycarpus dacrydioides*), and T. Worthy (unpubl. data) also argues for its inclusion. The addition of this species to List 2 would only strengthen the conclusions of this paper.

List 3. Additional taxa (apart from moas) accepted as forest birds in the pre-human avifauna are shown

in the third column of Table 2. Taxa marked with an asterisk (*) are usually accepted as forest birds. Of the remainder, *Porzana tabuensis* is now found in forest on Aorangi, one of the Poor Knights Islands (Onley 1982). Palaeoecological studies (e.g., Worthy & Mildenhall 1989) and analogy with living or recently extinct species (e.g., *Aegotheles*–Pizzey 1980; Olson et al. 1989) indicate that the species in column 3 of Table 2 can be considered to be forest birds. There was a considerable diversity of forest types in pre-human New Zealand, and some of these were reduced to relicts or perhaps extinguished by the Polynesian fires 600–800 years ago (McGlone 1989). It is reasonable to expect that many bird species preferred, or were confined to, specific forest types, and that not all the species referred to here as forest birds would be expected in a single forest type.

Nevertheless, there will always be some disagreement about palaeohabitat requirements for some species, even those such as the takahe (*Porphyrio mantelli*) which are still extant (Mills et al. 1984; Beauchamp & Worthy 1988; Mills et al. 1988). Although we can infer much from the resemblance of a fossil assemblage to present communities, and from knowledge of the habitat available within the catchment area of each site, it must not be overlooked that present communities contain a high proportion of recent immigrants and present populations of indigenous species may be occupying suboptimal, fringe habitat. Species in the pre-human fauna had very different selective pressures placed on them, and usually unknown ecological scope. The presence of rails in forest on predator-free islands suggests that their mainland habitat has contracted through community change and mammalian predation pressure. Other species, such as the rock wren *Xenicus gilviventris*, may well have occupied different habitats before mammalian predators restricted them to closed environments of rockpiles and scrub (Worthy & Mildenhall 1989).

List 4. List 4 comprises nine species of moas (Dinornithiformes) found in the South Island. Burrows (1980, 1989); Burrows et al. (1981); Anderson (1982, 1984, 1990); Worthy 1988, 1989b,

Table 2 South Island species accepted as forest birds by Flux (1989) and in this paper. List 1, those present in 1840 A.D.; List 2, species added in this paper; List 3, species extinct by 1840, but considered to be forest birds in this paper; List 4, South Island moa species. *–usually accepted as forest birds.

List 1	List 2	List 3	List 4
Apteryx australis	*Nestor notabilis*	*Cnemiornis calcitrans*	*Anomalopteryx didiformis*
Apteryx haasti	*Halcyon sancta*	*Euryanas finschi*	*Megalapteryx didinus*
Apteryx owenī	*Sceloglaux albifacies*	*Harpagornis moorei*	*Emeus crassus*
Gallirallus australis		*Circus [=~~Accipiter~~] eylesi*	*Euryapteryx geranoides*
Hemiphaga novaeseelandiae		*Porzana tabuensis*	*Pachyornis australis*
Strigops habroptilus		*Porphyrio mantelli*	*Pachyornis elephantopus*
Nestor meridionalis		*Gallinula hodgenorum*	*Dinornis novaezealandiae*
Cyanoramphus novaezelandiae		*Fulica chathamensis*	*Dinornis struthoides*
Cyanoramphus auriceps		*Aptornis otidiformis*	*Dinornis giganteus*
Cyanoramphus malherbi		*Coenocorypha aucklandica**	
Chrysococcyx lucidus		*Aegotheles novaezealandiae*	
Eudynamys taitensis		*Xenicus gilviventris*	
Ninox novaeseelandiae		*Traversia lyalli**	
Acanthisitta chloris		*Pachyplichas yaldwyni*	
Xenicus longipes		wren n. gen. n. sp.	
Anthornis melanura		*Corvus moriorum*	
Prosthemadera novaeseelandiae		+ List 1	
Gerygone igata		+ List 2	
Petroica australis			
Petroica macrocephala			
Turnagra capensis			
Mohoua ochrocephala			
Mohoua novaeseelandiae			
Rhipidura fuliginosa			
Philesturnus carunculatus			
Callaeas cinerea			

Totals: List 1, 27; List 2, 3; List 3, 16 including 6 rails and ducks, i.e., 10 "nonrails"; List 4, 9.

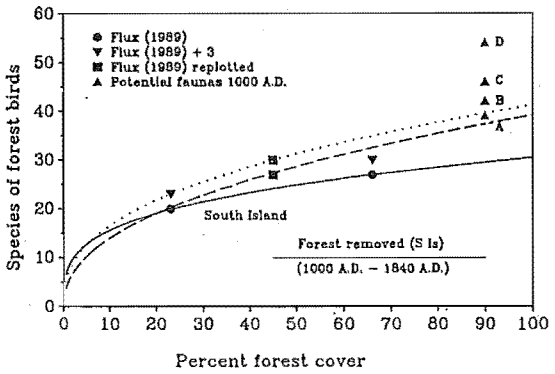

Fig. 3 Species of native forest birds known from New Zealand at A.D.1000, A.D. 1840, and at present, based on fig. 1 in Flux (1989). Solid line is curve as in Flux's figure; dashed line is this curve replotted to pass a revised point for forest cover and number of species at A.D. 1840 (see text); and dotted line passes through the revised point, using species number from List 2 (see text). The filled triangles represent potential faunas for the whole South Island before man's arrival, comprising: A, List 1 plus species from List 3 which conform with Slud's (1976) definition of land bird, except that *Euryanas finschi* is included; B, total for A, plus species in List 2; C, total for Lists 1–3, i.e., including all species accepted here as forest birds, except the moas; D, total for C plus all 9 South Island moas.

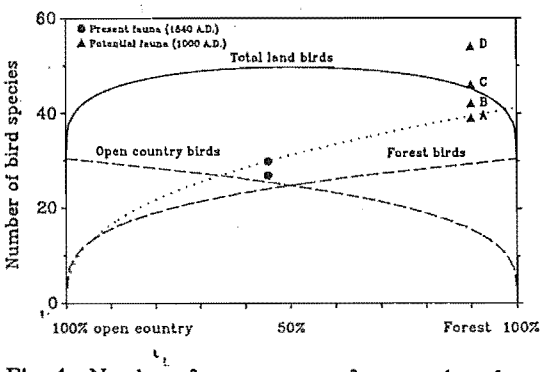

Fig. 4 Number of open-country, forest, and total terrestrial bird species expected and known in New Zealand, against relative proportions of open and forested land. Fig. based on fig. 2 in Flux (1989); present (A.D. 1840) and fossil (A.D. 1000) assemblages, and dotted curve through List 2 1840 value, added. Lettered filled triangles as in Fig. 3.

1990); and Worthy & Mildenhall (1989) have discussed the ecology of moas and suggest that most, if not all, species occupied forests, forest margins, or shrubland, although others, such as Batcheler (1989), have argued otherwise. Only *Pachyornis australis* and perhaps *Megalapteryx didinus* seem to have preferred higher altitudes, above the treeline in some areas. Even there, though, there would have been shrubs and herbs as well as grasses available as food.

Other taxa with claims to have inhabited forest before mammalian predators were introduced include: paradise shelduck (*Tadorna variegata*), by analogy with a species of *Tadorna* which is found in forest, and perches in trees, on some islands near New Guinea (J. M. Diamond, pers. comm.); *Anas aucklandica* (reported by Williams (1964) to have mainly inhabited swamp forest); and *Gallirallus philippensis* (which lives in low forest on small islands near Stewart Island; Kinsky 1970).

Fig. 3 is based on fig. 1 of Flux (1989), but for clarity only the South Island curve is plotted. The x-axis indicates the percentage of land area under forest cover, a value that differs little from the percentage of original forest cover because the South Island was probably about 85–90% forested in pre-human times (McGlone 1989). In Flux (1989), the point corresponding to number of forest bird species in the South Island in 1840 is plotted at 66% of original forest cover (North Island plus South Islands). I have replotted the point at 45% forest cover because McGlone (1989) has indicated that about 50% of the South Island forest cover present in pre-human New Zealand had been removed by the time Europeans arrived. Species in List 2 are plotted above Flux's values, for both 66% and 45% forest cover. The total number of forest bird species for the South Island, based on but not corresponding to the lists above, are plotted at 90% forest cover.

Point A (Fig. 3, 4) represents a conservative estimate of the number of forest species excluding the moas, the most contentious group: it includes all species in List 1 plus those in List 3, except *Cnemiornis, Porphyrio, Gallinula,* and *Fulica*. It therefore conforms to Slud's (1976) definition of land birds except for including *Euryanas* for which there is abundant evidence that it was primarily terrestrial. For B, the species in List 2 were added, and C includes also those species omitted on Slud's criteria but regarded here as terrestrial. D represents the total South Island forest avifauna, if all nine species of moa are included.

The curve plotted through Flux's points falls well below the potential values for the whole island, but curves fitted through present and replotted 1840 points pass near the lowest points. Smaller total

forest areas at A.D. 1000 would steepen both curves and bring them closer to the totals predicted here.

Figure 2 of Flux (1989) is reproduced here as Fig. 4. Points corresponding to species number in four potential faunas and the replotted 1840 point shown on Fig. 3 have been added, as well as the line fitted through the higher estimate of 1840 forest bird species. The number of terrestrial species (including those omitted by Slud (1976) in the potential faunas agreed closely with that predicted on the basis of an even mix of forest and open-country species on Flux's original plot. If the open-country and total land bird curves were also replotted, however, assuming equal numbers of forest and open-country species, the total land fauna would reach at least 60 species. Although further species will probably be found, it is unlikely that the total terrestrial avifauna for the whole South Island was greater than 50 species in the Holocene. The number of open-country species did not reach that predicted by the model.

DISCUSSION

I have assumed a direct relationship between the composition of fossil faunas at the four sites and that of the living communities they represent. This represents an ideal situation, unlikely to be approached in practice because of the vagaries of deposition and preservation. The relationship has never, to my knowledge, been studied under New Zealand conditions. The taphonomy of New Zealand fossil sites has only recently come under critical study, and there are few data available on the relative trapping efficiencies of swamps and caves for different bird species. I believe, however, that the trends in the data reflect the actual changes in the avifauna, because most of the biases in the fossil data will lead to an underestimation of both potential (H_{max}) and realised (H') diversity.

Some species which could reasonably be expected to be present and breeding in the catchment area of a deposit are, for unknown reasons, not represented in that fossil assemblage. The rarity of small passerines at Poukawa is an example. Flighted species are generally under-represented in cave and swamp deposits because they either do not enter the fossil trap, or they can readily escape if they do. Flightless species are often over-represented in such deposits, for obvious reasons. When and how long the deposit structure acted as a trap, and its ability to sample the fauna present in the area also produce biases in the record at a site: forest birds may be less well represented in a swamp deposit than waterbirds, although being abundant only a few tens or hundreds of metres away.

At the Washpool site, both species represented and numbers of individuals were directly related to human dietary preferences (Leach 1979). Chance is also an important factor, as is absolute abundance of a species in the living community. Many fossils of small acanthisittid wrens are known from cave deposits in both main islands, but only two specimens of an undescribed long-billed species have been found so far (P. R. Millener and T. H. Worthy, pers. comms.). Was this bird really rare in the unmodified community that the trap sampled, or did its habits and climbing ability keep it away from caves or enable it to escape from them easily?

The values of H' calculated for fossil assemblages are comparable with those for living faunas, and increased slightly with H_{max} as expected. The lower than expected increase probably resulted from factors such as poor representation of flighted, arboreal, and rarer species and dominance of flightless species. The slightly lower mean evenness value for the fossil assemblages supports this explanation for the lower slope of the combined fossil and present curve, because there is no a priori reason to suspect that bird communities in undisturbed forests should have different overall patterns of abundance than present communities. If evenness was higher, H' would have been higher too.

The Shannon Index was shown to be highly correlated with total species number for the fossil assemblages, as expected from other studies. It was used here purely to facilitate direct comparisons with the published work.

McLay's (1974) prediction of $H_{max} = 2.5$ for the diversity of forest birds in the pre-European fauna is too low if "pre-European" is extended to the "pre-human" situation. At any one site and time, the potential H_{max} was up to 3.5, and the realised H' at least 2.1–2.9. Allowing for the biases in deposition, it is clear that the Shannon diversity of New Zealand forest birds has declined over the past 1000 years, although there are still extensive areas of forest remaining, particularly on steep lands.

Even if the relationship between species number and forest area today is accurately modelled by the curve in Fig. 3, the considerable positive deviation from the expected number in the fossil communities must be explained. Either some or all of the extinct species included in the forest bird totals were not forest dwellers, or New Zealand had disproportionately more forest bird species than other islands.

Flux (1989) takes the first view; the second is supported by the paucity of native open-country birds in either the present or fossil assemblages. Compared with the large fauna of obligate grassland birds in Australia, a fauna which includes many parrots and grass finches, the modern New Zealand open-country avifauna is, and was, depauperate. It may be that, contrary to present expectations, the number of extinct passerines has been grossly underestimated (J. M. Diamond, pers. comm.) because the small gauge screens necessary for their detection have not been used routinely in New Zealand excavations. If, as Diamond suggests, the fossil avifauna was twice as large as we presently think, then the apparent lack of open-country species may be an artefact of collecting. Few, if any, sites laid down in open-country (i.e., grassland) have been excavated yet. In any event, such a large increase in extinct taxa would only exacerbate the present difference between biogeographic, theory estimates of New Zealand bird diversity, and the empirical data.

Diamond (pers. comm.) also points out that it is very difficult to calculate the expected number of species for a temperate Pacific island of New Zealand's size, because the base work has not been done for Australia and nearby islands. This is not attempted here, because the discussion centres on Flux's use of Slud's analysis, but such a study may well provide new insights into what may be expected, if not in Holocene deposits, then in Miocene and early Pleistocene faunas of New Zealand.

Keas (*Nestor notabilis*) penetrate high altitude fellfields and riverbeds. Pipits (*Anthus novaeseelandiae*) certainly live in tussock grasslands, but it has been suggested that they require taller vegetation in their territories (Bull, in Hamel 1972), or at least higher rainfall or humidity, than the introduced skylark (*Alauda arvensis*) (Hamel 1972). The extinct quail (*Coturnix novaezealandiae*) was apparently associated with open tussock grasslands. The harrier (*Circus approximans*) can hunt effectively in closed kanuka (*Kunzea ericoides*) forest (pers. obs.; H. Cameron pers. comm.) but prefers grassland; it is rare in deposits older than 1000 years. There is considerable empirical evidence from faunal associations and vegetation prevailing at fossil sites during deposition, that species such as Haast's eagle (*Harpagornis moorei*) and owlet-nightjar (*Aegotheles novaezealandiae*) which Flux and McLay assumed to have inhabited open-country, lived in some forest types. McLay's comment that "It is significant that no native forest birds are known only from sub-fossil remains", although in keeping with the popular view of the time, is incorrect, as shown, for example, by the acanthisittid wrens.

The point is, that even if we accept half of the moas as open-country birds, the total number of such species will not match that predicted or assumed in the model. Therefore the curves in Fig. 4 will be strongly skewed to the right. Flux's contention, on biogeographic grounds, that many of the extinct species were open-country birds, is not supported by the empirical data on fossil faunal and floral assemblages.

If some groups in the pre-human avifauna were restricted by the small extent of their preferred grassland habitat in the Holocene, they should not have declined as rapidly as they did when the grasslands expanded dramatically 500–800 years ago, even allowing for the intensity of human predation (Anderson 1989). If some or all moas were grassland birds, their habitat increased by several hundred percent. Similarly, the increase in grassland should have increased the habitat available to the takahe (*Porphyrio mantelli*), if it were a true grassland species. There is no firm basis on which to predict that even half of moa species inhabited open-country.

It is here that palaeoautecological studies must take over. Worthy (1990) suggests on distributional and faunal grounds that two of the nine species of moa in the South Island—*Megalapteryx didinus* and *Pachyornis australis*—inhabited open high country habitats. Two others, *Anomalopteryx didiformis* and *Dinornis novaezealandiae*, were common in the wet western forests during the Holocene. The other species were abundant to the east of the main ranges, in drier forests and shrubland.

Zimmerman & Bieregaard (1986) pointed out in another context that even for living communities, autecological studies often allow far better predictions of presence or species numbers in habitats than do simple species-area relationships.

If we accept that the pre-human avifauna *was* dominated by forest species, the high rate of extinction in the fauna in the period before European settlement must be related to the characteristics of the forest areas removed in that period. These forests were mainly the drier, eastern forests, or those in inland areas where drought or severe climate restricted regeneration after clearances (McGlone 1980, 1983, 1989). This applies to both main islands. I have discussed this elsewhere (Holdaway 1989) and suggested that it was the drier, more structurally diverse forests on more fertile soils which supported

the greatest diversities of birds in pre-human times. The maximum diversity was attained in western and northern areas only when climatic conditions favoured vegetation other than tall, wet forest. Even in the wetter forests, the fall in diversity of birds probably accompanied, and may have caused, a change in the structure of the forests themselves. As Wardle (1986) noted that "We must now accept that the pre-Polynesian forests of New Zealand could have been as different from the forests of the immediately pre-European era as the latter were from the native forests of today".

The total number of terrestrial bird species in the pre-human fauna agrees closely with Flux's prediction only if rails and ducks are excluded. Slud's (1976) criteria for land birds do not appear to hold for island faunas, particularly where mammalian predators are absent. It may be simpler not to consider groups such as the rails species by species, but these groups bridge the division between terrestrial and indeed forest habitats and freshwater habitats. Waterfowl, too, can be primarily terrestrial. Even in Australia, where mammalian and reptilian predators are, or were, abundant, the maned goose *Chenonetta jubata* spends much time far from water. Similarly, the Hawaiian goose *Branta sandvichensis* is terrestrial.

It is important to consider each species separately when assessing the palaeohabitats of New Zealand birds. To ignore the rails and waterfowl seriously biases the data in island ecosystems. A better understanding of changes in diversity with time, and of faunal composition and habitat requirements is important, not only for theoretical biogeographical reasons, but as a basis for management of the remaining forest biota.

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CHAPTER 5

12. CHAPTER 5

ECOMORPHOLOGY OF HAAST'S EAGLE, *HARPAGORNIS MOOREI* (AVES: ACCIPITRIDAE)

12.1 INTRODUCTION

Since Haast (1874) and Owen (1879) pointed out that Haast's Eagle had a proportionately short ulna relative to that of the Wedge-tailed Eagle (*Aquila audax*) and other accipitrids, several authors have suggested that the bird could not fly well (Duff 1949) or spent much of its time on the ground (Millener 1984). In addition, it has been suggested that the eagle was primarily a carrion eater (e.g., McCulloch 1991; Millener 1984). I discussed the carrion hypothesis in Chapter 4 and concluded from the patterns of association with potential prey that Haast's Eagle was an active predator.

Another approach to both the problem of flying ability and that of predation potential (Voous 1969) is to compare the body conformation and proportions with those of other, living, raptors. The hypothesis is that obligate carrion feeders will have different morphometrics than active predators because the functional systems for each way of life are different. This can be tested by a multivariate analysis of skeletal dimensions encompassing all major body elements, for a range of species with known habits. If Haast's Eagle was an obligate carrion feeder, it should have had a body conformation similar to that of living carrion feeders.

In this chapter, I first examine the proportions of major skeletal elements of Haast's Eagle to see whether, as suggested by McCulloch (1991) and Millener (1984), its wings were smaller and its legs were larger than expected. If true, this would support the hypothesis that it had a tendency towards ground living, and perhaps carrion feeding.

Then through multivariate analysis of bone dimensions, I investigate which ecogroup Haast's Eagle most resembled, and which mode of flight it may have employed.

12.2 METHODS

Skeletal elements of a representative specimens from a range of large and small accipitrids were measured with Vernier calipers to the nearest 0.1 mm. Tables of measurements are given in appendices to this chapter.

12.2.1 Statistical treatment

Bivariate plots of element lengths were prepared to see if Haast's Eagle differed from other accipitrids in major proportions of bones. Femur length was used as a measure of body size (Alexander 1983; Prange *et al.* 1979), since tibiotarsus circumference, possibly a better indicator of body weight (Campbell & Tonni 1983), was difficult to measure accurately. Head length and head proportions, sternum and pelvis length, humerus and ulna length, and tarsometatarsus length were examined. Wing and leg bone dimensions were then "normalised" by dividing by femur length and the proximal elements of each limb were plotted against each other.

Although most body dimensions vary allometrically, the small sample and repetition of individuals within species precluded a full allometric analysis. Bivariate statistics were adequate for this analysis. I used partial correlation and multivariate regression routines from the BMDP6R package.

The physical robustness of various elements was examined by plotting distal width against length as a measure of slenderness.

Forty-nine skeletal dimensions of a range of large accipitrids, including several individuals of most taxa, were subjected to Principal Components Analysis (PCA) to detect any pattern in the overall structure of the various species.

Discriminant Function Analysis was used to examine the features separating two *a priori* locomotory groups, designated flappers and gliders on the basis of their normal mode of flight (e.g., Brown & Amadon 1968).

PCA and Discriminant Function Analysis were performed via the 4R and 7M routines of the BMDP statistical package, respectively.

Fig. 12.1 Wire and plaster model of (featherless) large specimen of Haast's eagle, for volume measurement by displacement. Model was varnished to lessen water absorption during brief immersion. Model based on bird represented by humerus AV 36396 (Hives extension, Honeycomb Hill) using interbone proportions developed from complete specimens.

12.2.2 Live weight

The weight of a large living Haast's Eagle was estimated from the volume of a full-sized model (Fig. 12.1) I made of an individual represented by bones from Honeycomb Hill, and from published allometric relationships between bone dimensions and body weight.

12.2.3 Claw size

The length, depth at base of claw, and depth over flexor process of pedal digit 1 ungual phalanges of a range of living and extinct large acciptrids were measured. The ratios of depth over flexor process and claw depth to length were calculated and compared.

12.3 RESULTS

12.3.1 Bivariate statistics and scatter plots

Cranium length was highly correlated with femur length, as was premaxilla length (Fig. 12.2: head length, $r^2=0.874$, $F=222.2$, $P<<0.001$). The dimensions of Haast's Eagle were as expected for an accipitrid of its body size (Fig. 12.2). Premaxilla length and depth were also within the expected range (Fig. 12.3).

One of the characters distinguishing Haast's Eagle from *Aquilas* is its narrow skull (Chapter 2; Oliver 1955). Postorbital width and cranial depth were both within the range of dimensions for other accipitrids, although postorbital width tended to be low (Fig. 12.4). Increased scatter at the high end of the size range lowered the correlation coefficients, but both measurements were still strongly correlated with body size as measured by femur length (cranial depth $r=0.782$, $F=50.24$, $P<<0.001$; postorbital width $r=0.763$, $F=44.51$, $P<<0.001$).

Sternum length and pelvis length were both below the expected values for birds of Haast's Eagle size when the distribution for living accipitrids was plotted against femur length (body size) (Fig. 12.5). However, there was a tendency for the distribution to bifurcate at about the mid range in body size (femur length 100-125 mm), and was particularly obvious in plots of humerus and ulna lengths against femur length (Fig. 12.6). Examination of the taxa involved with each branch of the bifurcation indicated that the upper limb contained birds that

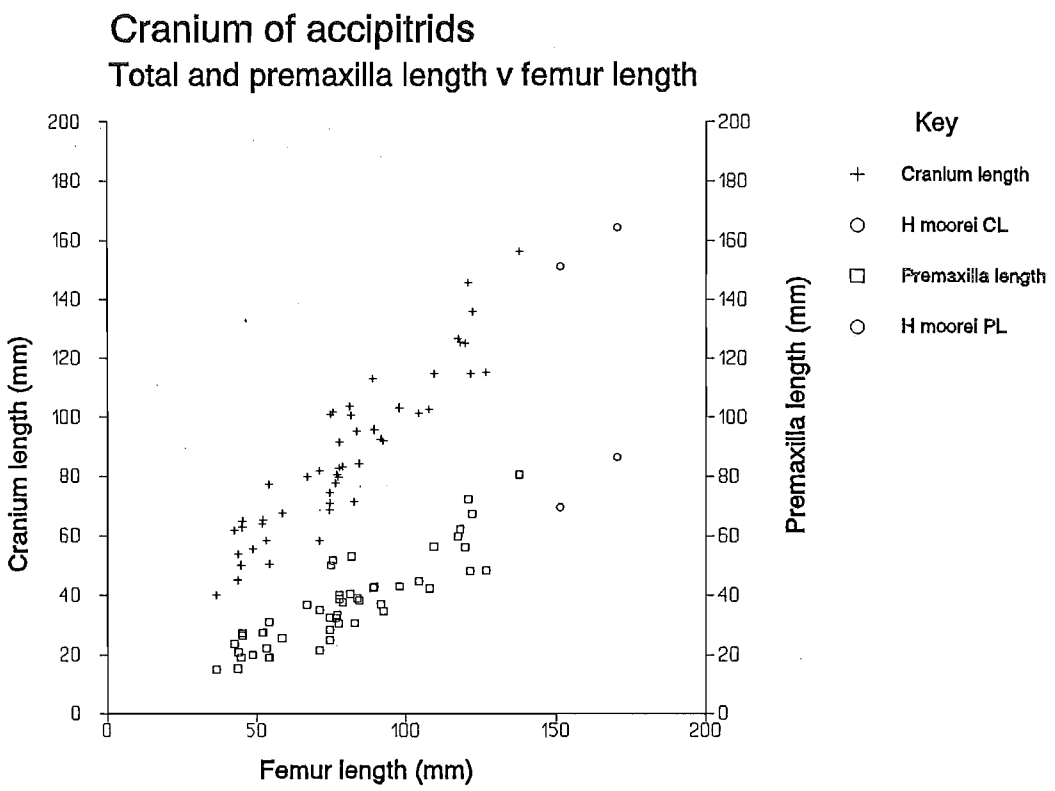

Fig. 12.2 Scatter plot of cranium and premaxilla lengths (mm) against femur length (mm) for a representative species from each of 45 genera of accipitrids.

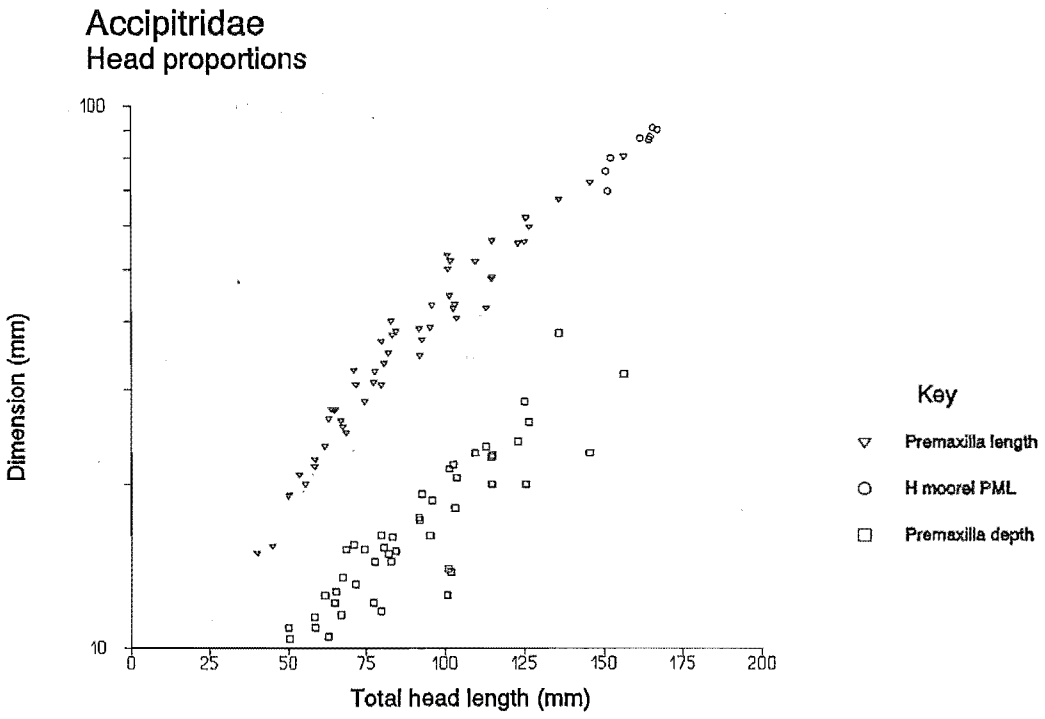

Fig. 12.3 Scatter plot of premaxilla length and depth (mm) against total heaaad length for a representative species from each of 44 genera of accipitrids. Note log-normal scale.

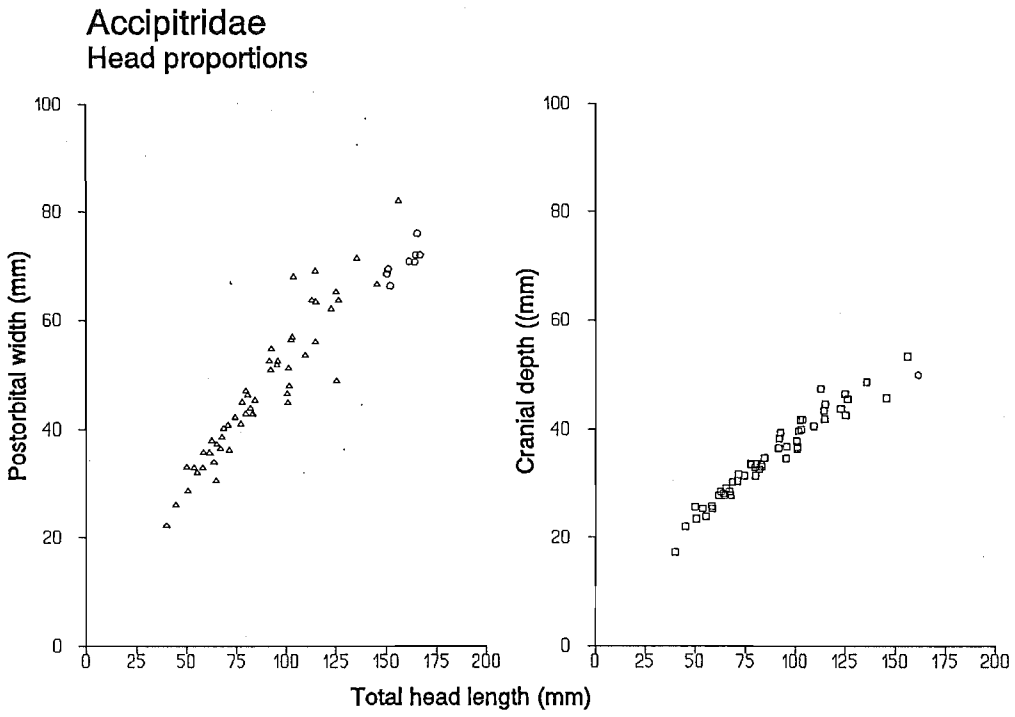

Fig. 12.4 Scatter plots of postorbital width and cranial depth against total head length for a representative species from each of 44 genera of accipitrids.

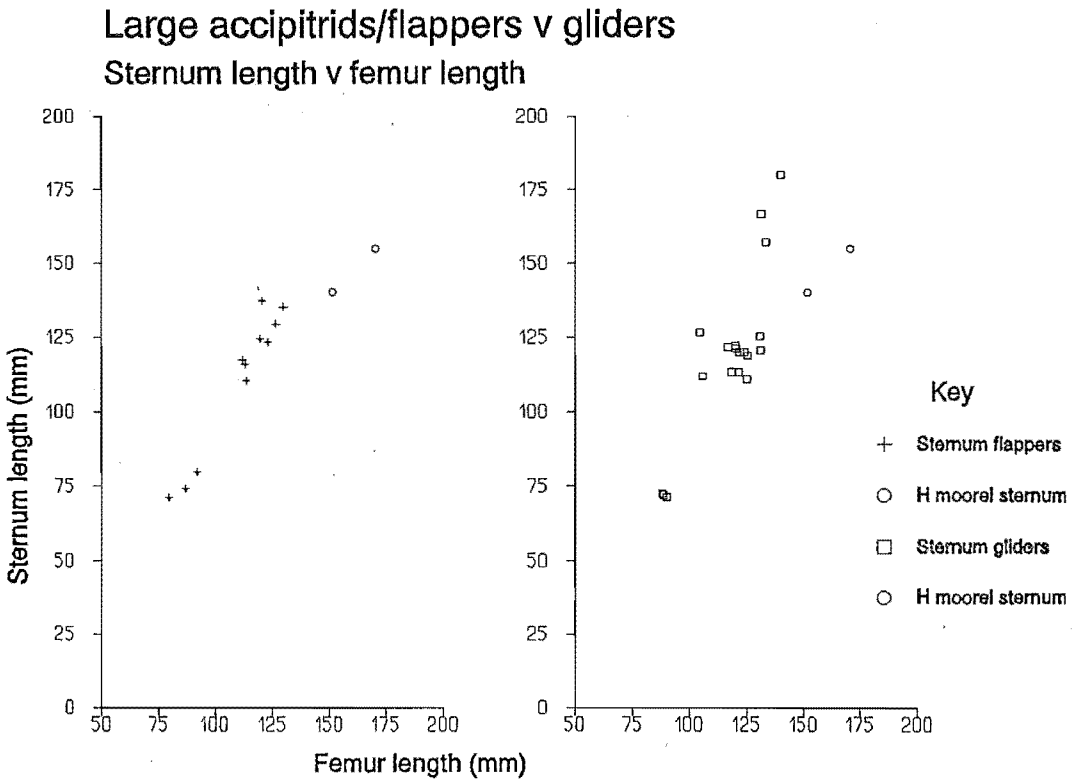

Fig. 12.5 Scattergram of pelvis and sternum length (mm) against against femur length for a range of large accipitrids.

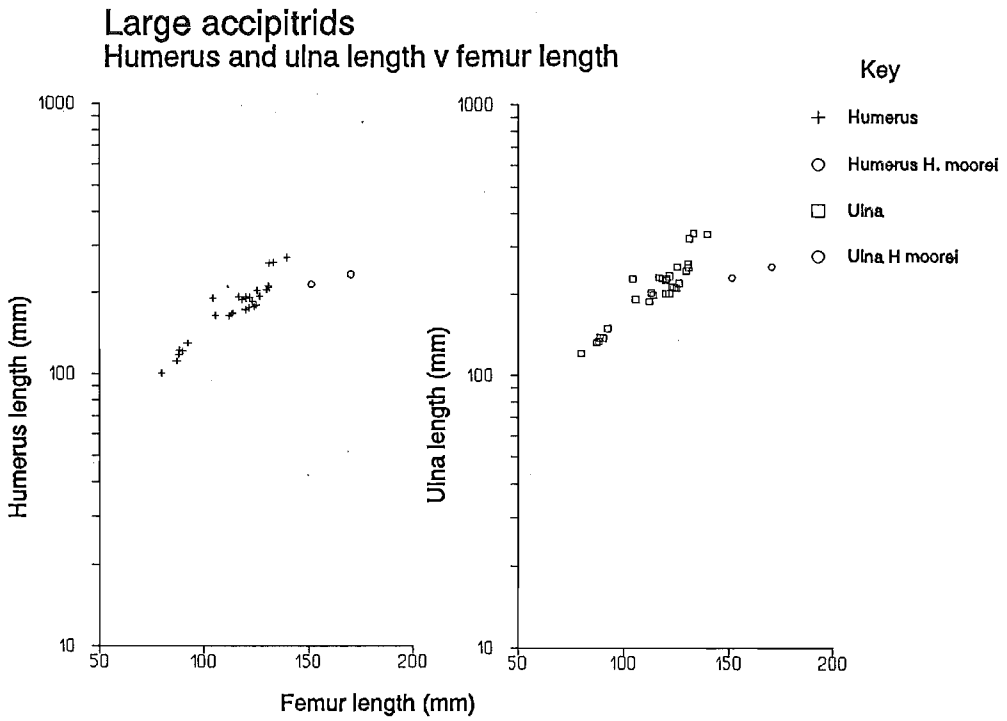

Fig. 12.6 Scattergram of humerus and ulna length (mm) against femur length (mm) for a range of large accipitrids.

habitually glide, and the lower limb consisted of species that flap, or flap and glide. Haast's Eagle represented the extremity of the flapping limb (Fig. 12.6).

To test whether femur length influenced the distribution of wing proximal element lengths, I replotted humerus and ulna lengths against tibiotarsus shaft diameter (Campbell & Tonni 1983). As can be seen in Fig. 12.7, the bifurcation between flapping (lower cluster) and gliding (upper cluster) species was even more pronounced when this was done. Again, Haast's Eagle was the terminal taxon on the flapper limb.

A plot of tarsometatarsus length against femur length (Fig. 12.8) indicated that the length of this element in Haast's Eagle was as expected for a bird of its size. Tarsometatarsus length was also significantly correlated with femur length ($r=0.84$, $F=76.67$, $P<<0.001$), and tibiotarsus length was even more strongly correlated with femur length, as might be expected considering its functin as a vertical supporting strut beneath the cantilever of the femur ($r=0.932$, $F=213.21$, $P<<0.001$).

Wing bone proportions in Haast's Eagle were not unusual, despite the relatively short ulna. Plots of 'normalised' ulna and carpometacarpus lengths against 'normalised' humerus length for a range of large accipitrids (Fig. 12.9) indicated a strong association between them (ulna v humerus, $r=0.9904$). The point for Haast's Eagle fell slightly below the regression, but at 1.44 it was within the 95% confidence limits (1.41, 1.80) for its humerus length. Including the Haast's Eagle point did not degrade the correlation coefficient (0.9881 as against 0.9904). The ulna length was near the low end of the range, and between those of three forest eagles. The vultures (*Aegypius, Gyps*) and sea eagles (*Haliaeetus*) were at the opposite end of the range for both ulna and carpometacarpus lengths (Fig. 12.9).

'Normalised' carpometacarpus length for Haast's Eagle fell within the scatter for other accipitrids, but at the low end of the range (Fig. 12.9).

In contrast, there was no clear trend in the distribution of leg element length ratios (Fig. 12.10). The point for Haast's Eagle is in the centre of the distribution, next to that for *Harpia harpyja*, the Harpy Eagle (Fig. 12.10). Furthermore, forest and open country species (flappers and gliders respectively)

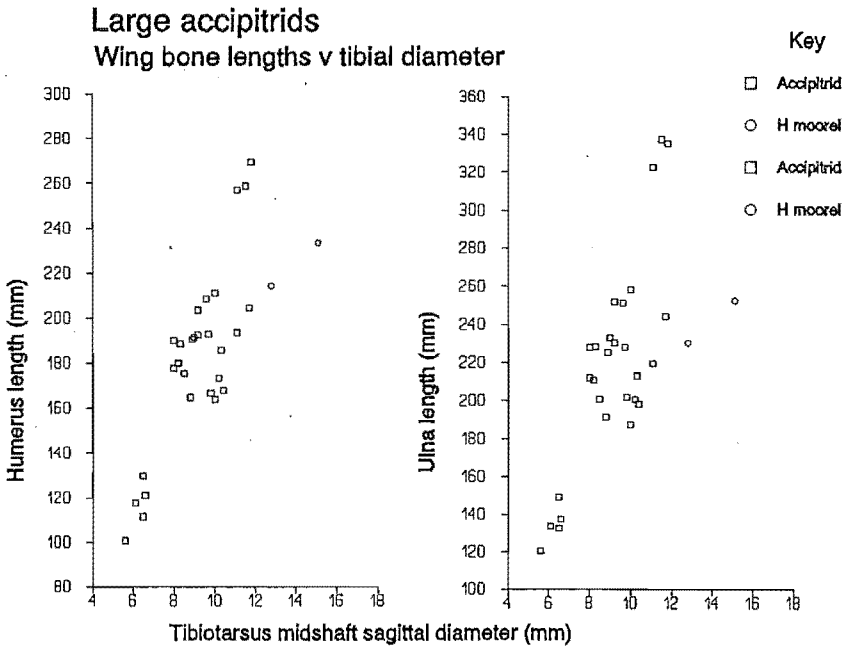

Fig. 12.7 Scattergram of humerus and ulna length (mm) against tibiotarsus midshaft sagittal diameter (mm).

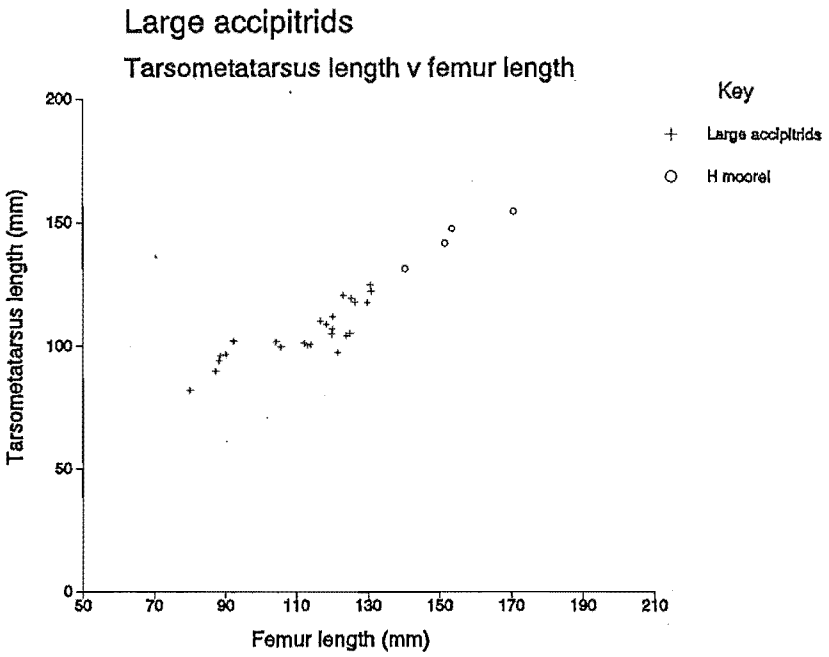

Fig. 12.8 Scattergram of tarsometatarsus length (mm) against femur length (mm) for a range of large accipitrids.

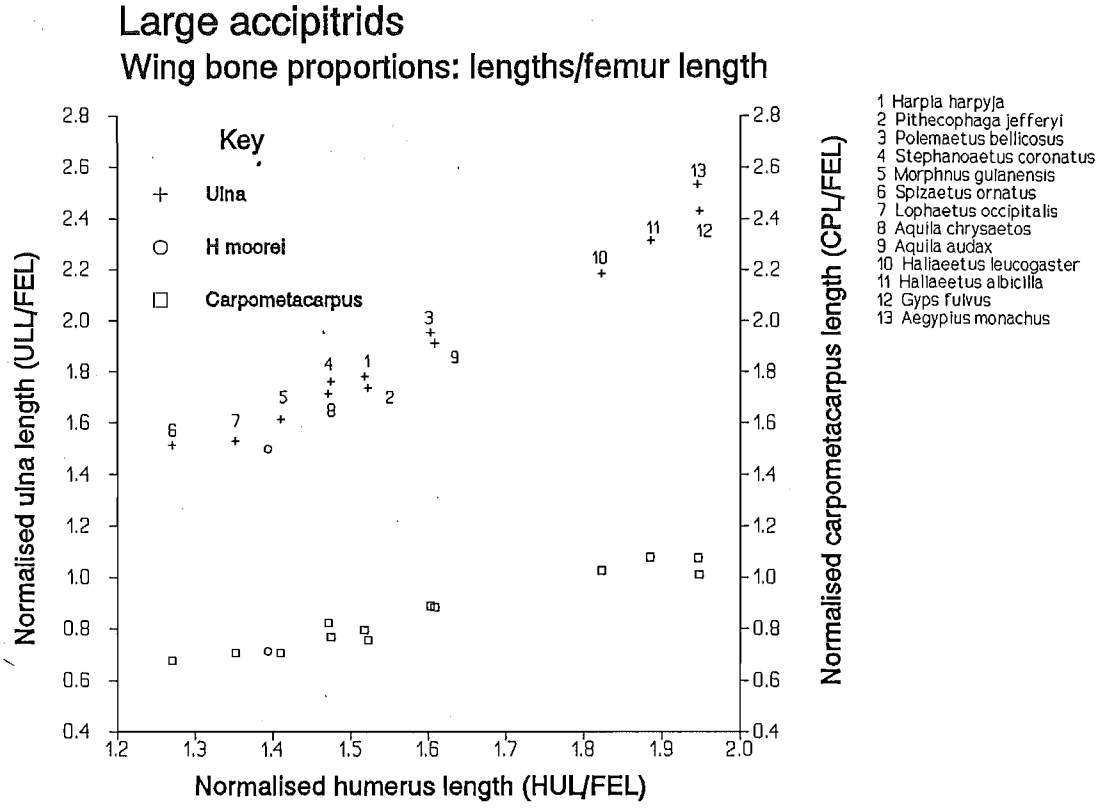

Fig. 12.9 Plot of main wing element lengths, corrected for body size by dividing by femur length, for a range of large accipitrids.

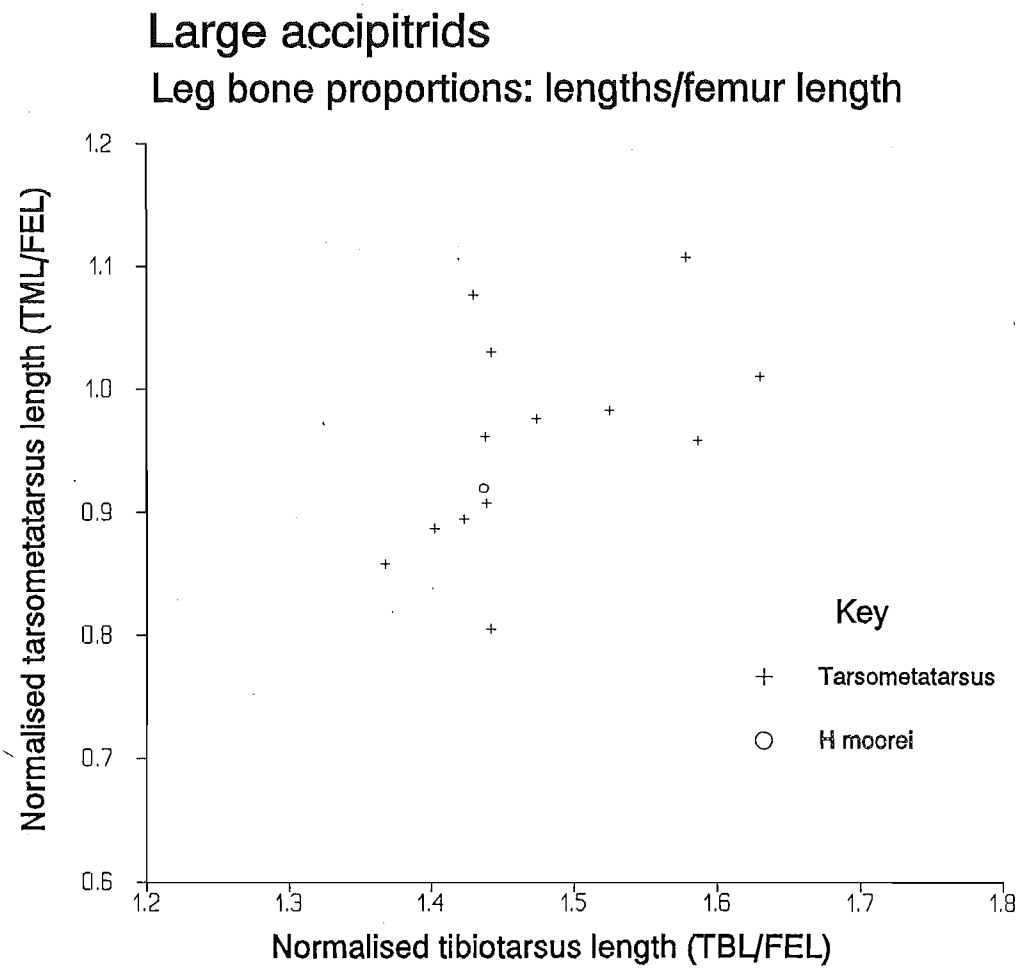

Fig. 12.10 Plot of tarsometatarsus length against tibiotarsus length, both corrected for body size by dividing by femur length, for a range of large accipitrids.

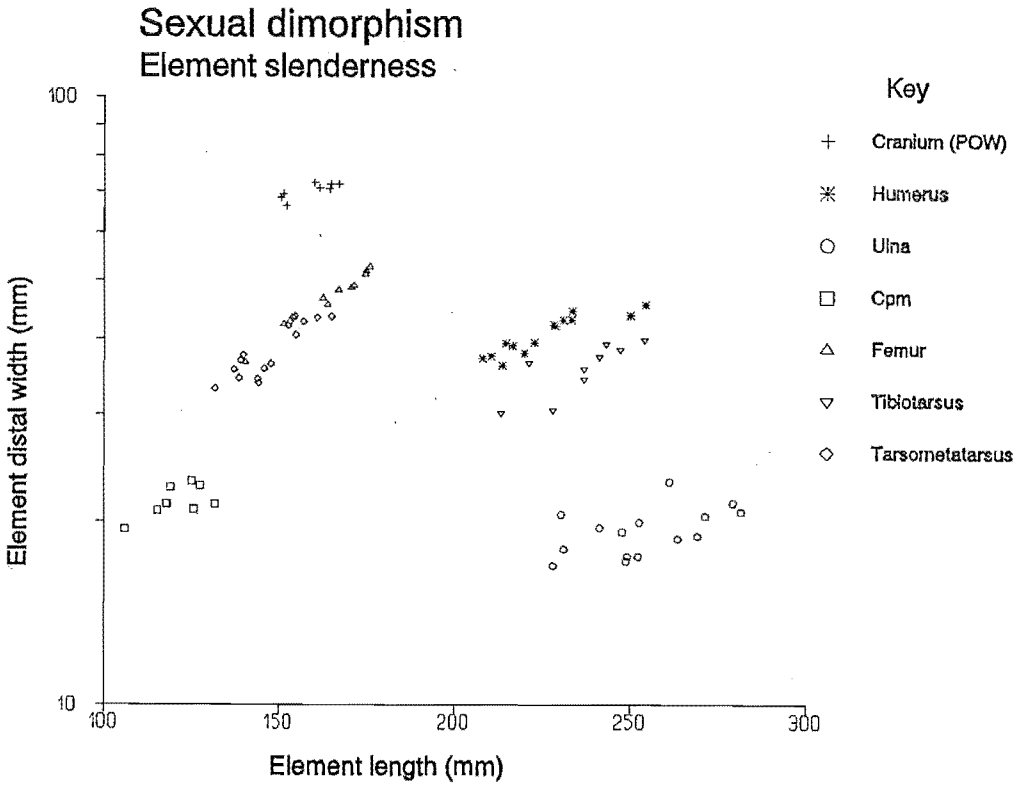

Fig. 12.11 Sexual size dimorphism as indicated by plotting slenderness (distal width (mm) against length (mm)) for main limb elements and crania of a range of large accipitrids. Note log-normal scale.

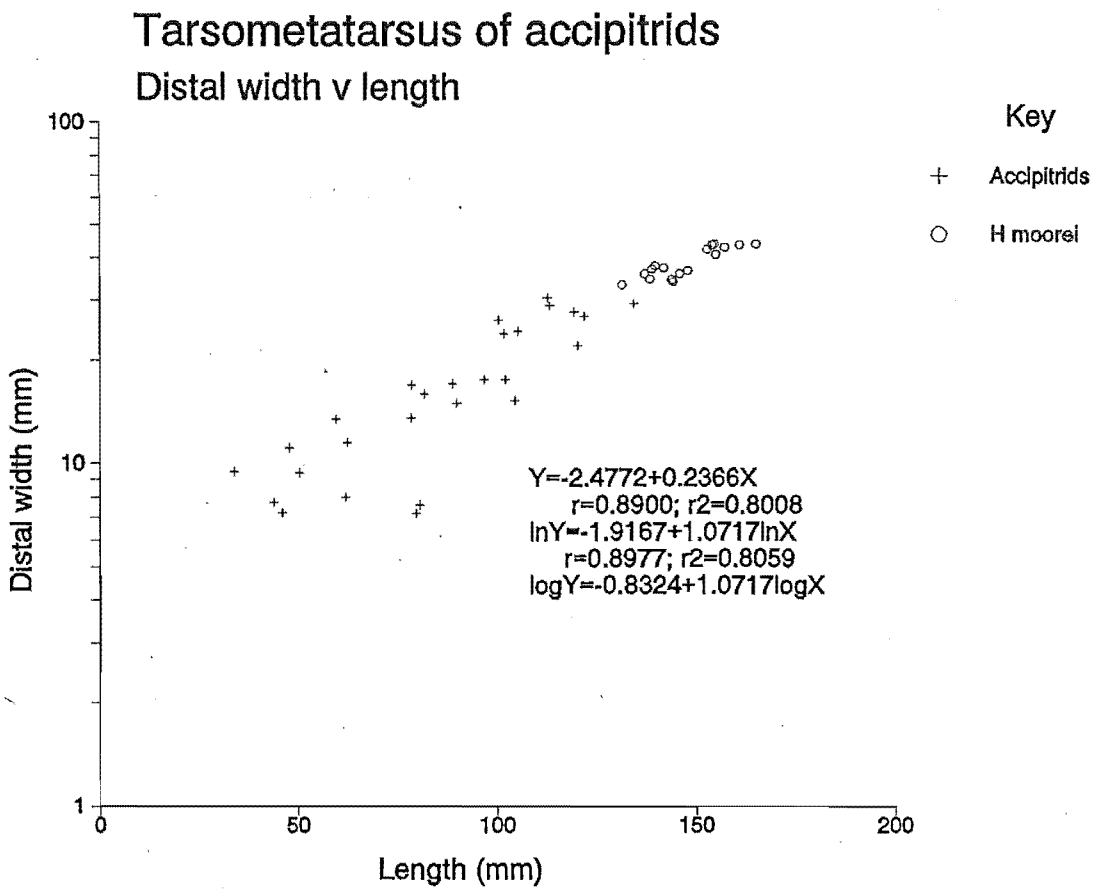

Fig. 12.12 Limb bone slenderness and sexual dimorphism. Distal width of tarsometatarsus (mm) against length (mm) for a range of accipitrids. Note log-normal scale.

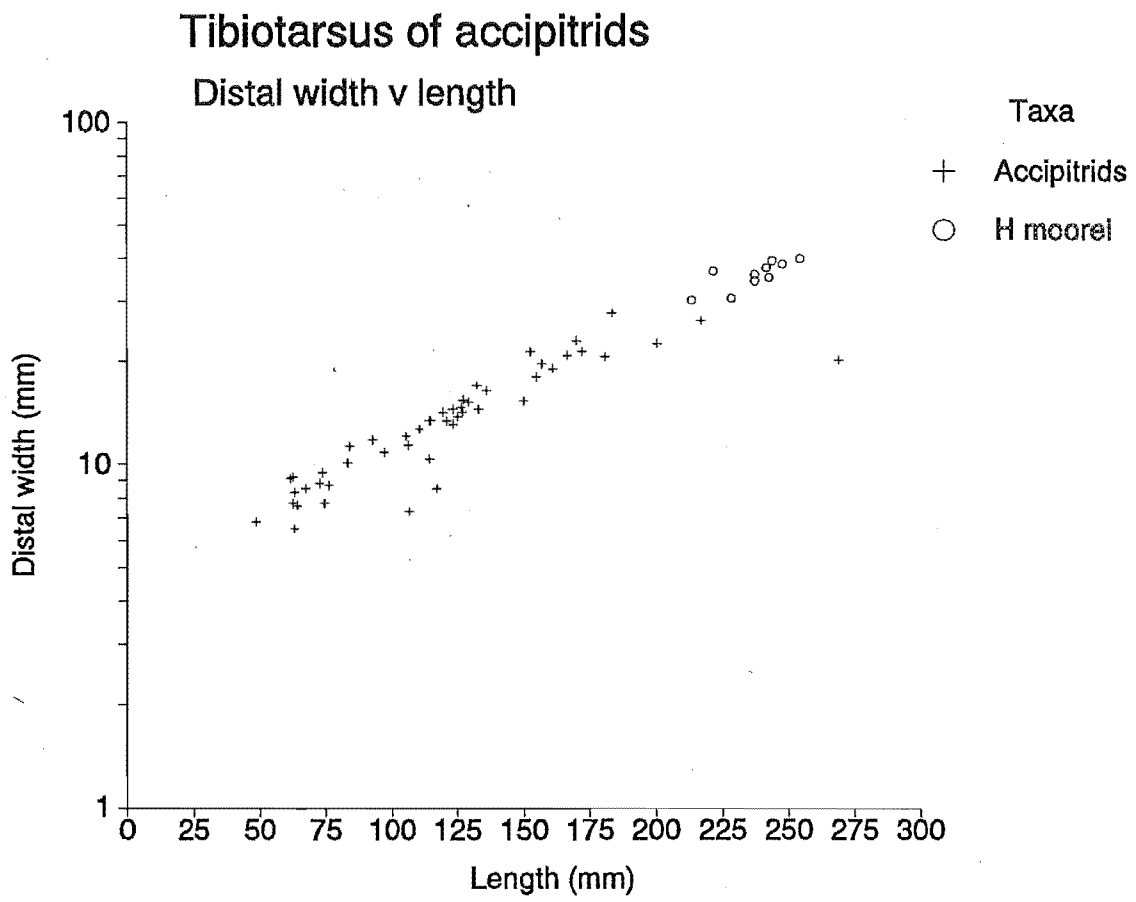

Fig. 12.13 Limb bone slenderness and sexual dimorphism. Distal width of tibiotarsus (mm) against length (mm) for a range of accipitrids. Note log-normal scale.

were intermixed, again in contrast to the situation observed for wing proportions.

Most elements of large accipitrid skeletons have similar proportions, probably because of the structural requirements of long elements in bending and torsion. A plot of distal width against length for various limb elements and the cranium thus show little spread (Fig. 12.11). However, some dimorphism in robustness of the head and tarsometatarsus is evident. This bimodal distribution of slenderness, apparently between the sexes, may be related to differences in diet, as males and females of dimorphic species tend to take different size ranges and sometimes different taxa of prey (Newton 1979).

The separation of what were apparently the two sexes based on tarsometatarsus proportions was especially marked in Haast's Eagle (Fig. 12.12). This was not so clear in the tibiotarsus (Fig. 12.13). Individual tarsometatarsi formed two distinct clusters at the upper end of the size range in both length and distal width.

12.3.2 Principal component analysis

Plots of the first three principal components of an analysis of 49 element lengths for 15 taxa of large accipitrids placed Haast's Eagle near the Harpy Eagle, and away from the *Aquila* eagles (Golden and Wedge-tailed), which clustered together (Fig. 12.14). The accipitrid vultures *Aegypius* and *Gyps* were together at the other end of the cluster pattern. The closest taxa to Haast's Eagle in 3-dimensional component space were two other very large forest eagles, the African Crowned (*Stephanoaetus coronatus*) and the Philippine (*Pithecophaga jefferyi*) (Fig. 12.14). The large spread in the distribution of both the Harpy and Haast's Eagle, presumably indicates sexual differences: Haast's Eagle and the Harpy overlapped on the first two components.

Eigenvalues declined sharply after the second, and the first three principal components accounted for 93.52% of the total variance in the data. The first principal component was related to general body size, with the large vultures and Haast's Eagle scoring highest, and the small South American *Morphnus*, and *Spizaetus*, and the African *Lophaetus* scoring lowest. Low values of principal component 2 were associated with increasing claw size, and robustness of the leg

bones, whereas higher values of this component were associated with longer wings and smaller claws.

Separation on the third component was related to increased distal wing length (mainly the carpometacarpus) and a broader head (positive PC values), against larger, broader posterior pelvis and legs (negative PC values).

12.3.3. Discriminant function analysis

The factors characterising the groups found in the bivariate and PCA analyses were investigated by Discriminant Function Analysis, using *a priori* groups of flappers and gliders.

When Haast's Eagle was classified as a flapper, analysis of whole body dimensions, and head and wing element dimensions considered separately, resulted in its being maintained in the flapper group. However, the factors discriminating between the groups did not include ulna length, the characteristic most quoted as indicating a trend towards flightlessness. When Haast's Eagle was omitted from the all dimension analysis, the discriminating variables were mandibular symphysis length, humerus shaft diameter, carpometacarpus length, proximal pelvis width, pelvis waist width, pygostyle length, and the medial and sagittal tibiotarsus shaft diameters. The standardised coefficients from the discrimination function were -1.465, 5.542, -5.711, 2.056, -3.406, -2.938, 8.96, -3.894, respectively. The calculated loadings for Haast's Eagle placed both complete specimens with the gliding group.

When the dimensions of Haast's Eagle were contrasted with those for all members of the flapper and glider groups, the canonical variable plot showed Haast's Eagle to be a 'super flapper', on the opposite side of the main flapper distribution from the gliders (Fig. 12.15). The canonical variables that discriminated between taxa when Haast's Eagle was contrasted with the others included ulna length, which had a strong negative standardised loading. The other factors were cranial depth, postorbital width, mandible length, pelvis acetabular width, pygostyle length, femur proximal width, and tarsometatarsus length. The postcranial factors are associated with flight mode (ulna and pygostyle length) or grip strength (pelvis and femur width).

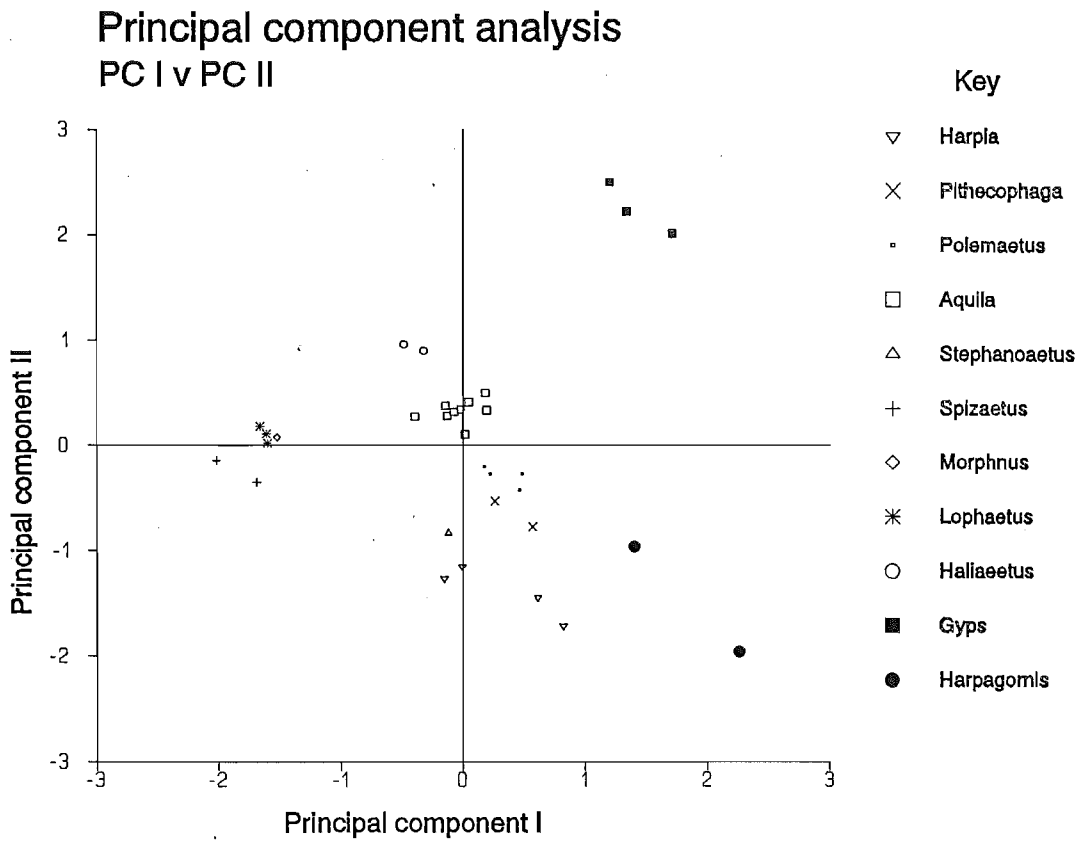

Fig. 12.14 Bivariate plot of first two principal components from PCA analysis of 49 skeletal measurements of representatives individuals from one or more species from each of 11 genera of large accipitrids.

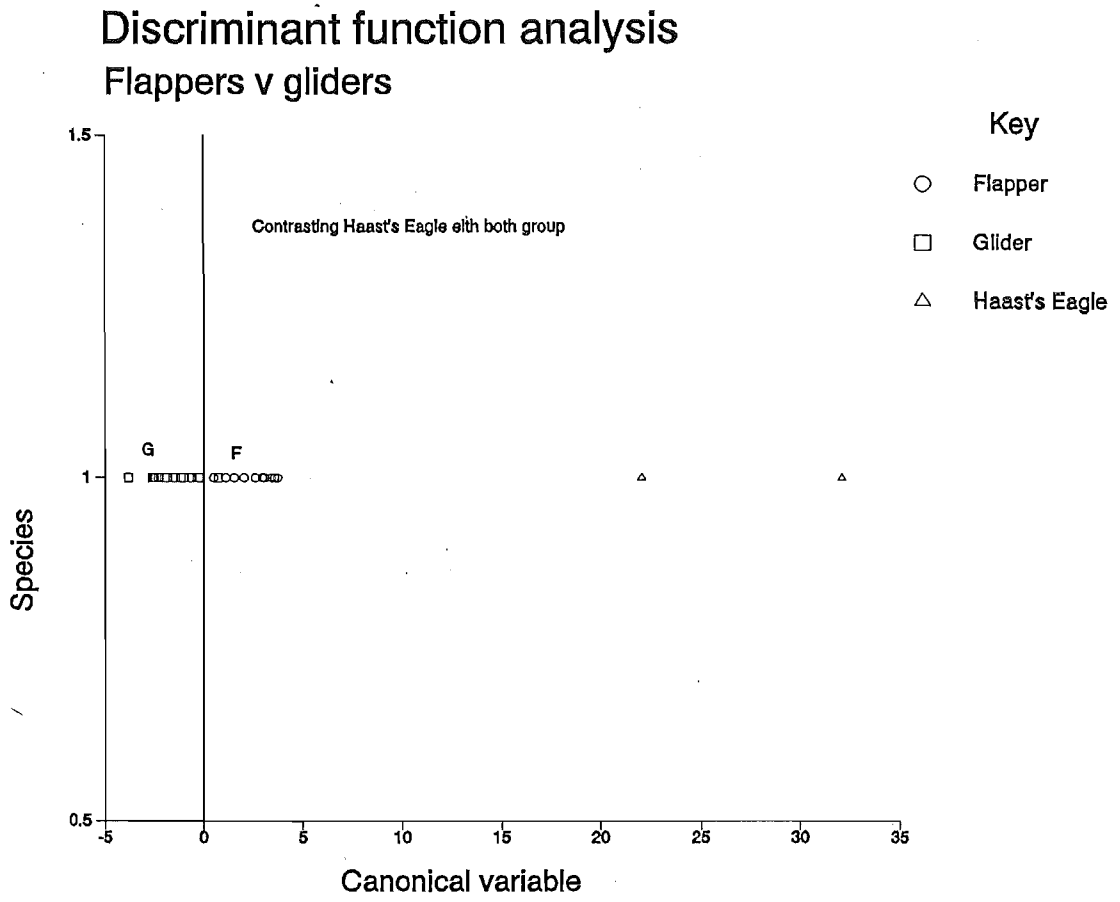

Fig. 12.15 Plot of standardised canonical variable for Discriminant Function Analysis of skeletal dimensions, contrasting Haast's Eagle with other large accipitrids.

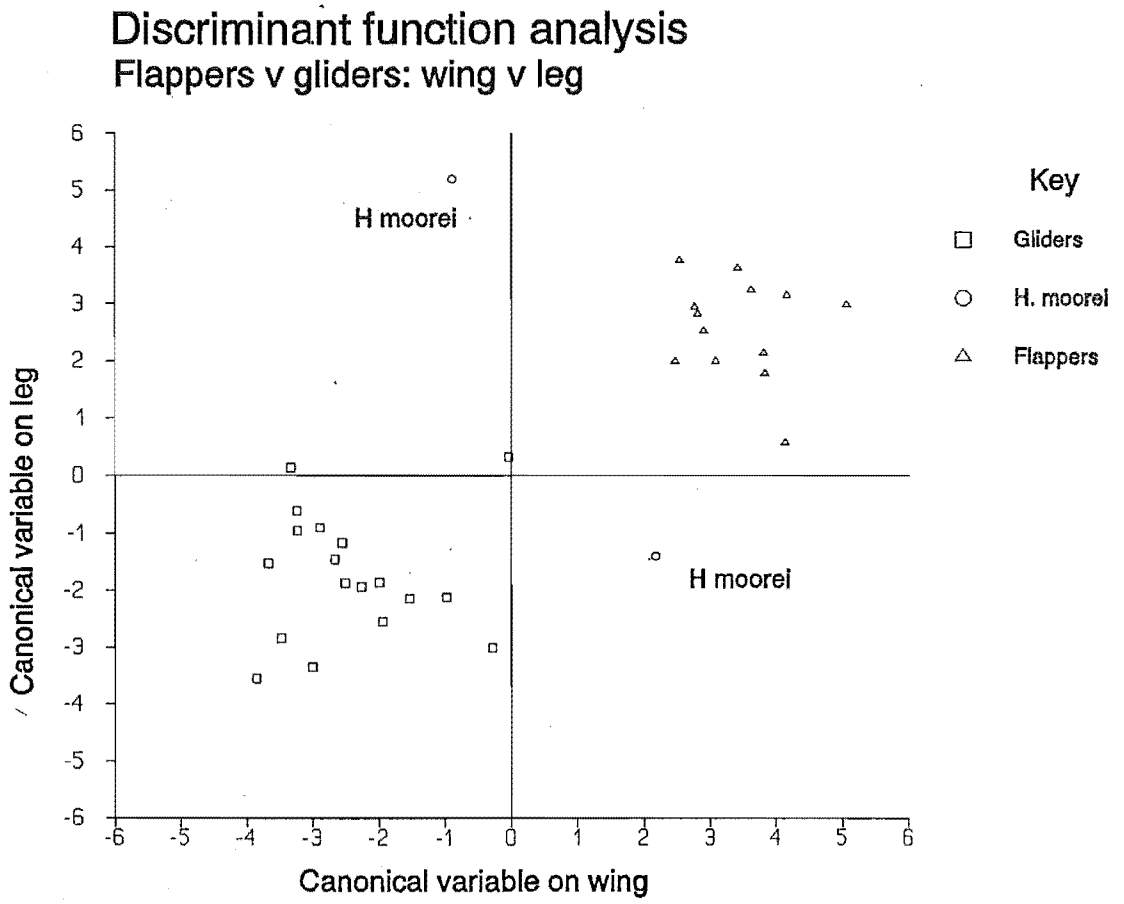

Fig. 12.16 Plot of canonical variables for wing bones against those for leg bones, from Discriminant Function Analysis of skeletal dimensions of large accipitrids.

A plot of canonical variables on wing dimensions against those derived from leg element dimensions gave two clusters, corresponding to flapper and glider groups, but the two individual Haast's Eagle specimens were separated, on either side of the axis joining the main groups (Fig. 12.16). The leg dimensions of one bird were closer to those of flappers and those of the other were closer to the gliders; the opposite applied to wing dimensions. This suggests that the two individuals had different proportions, and therefore could even have had different flight modes and prey! If the two individuals represent different sexes, as other evidence presented in Chapter 2 suggests, then the sexes of Haast's Eagle may have been more dimorphic in behaviour and feeding habits than other raptor species.

12.3.4 Live weight

12.3.4.1 *Displacement model* The full-scale model displaced 0.0124 ± 0.0001 m^3 (mean of 2 immersions), corresponding to a weight (without feathers) of 11.64 kg. Allowing for feather weight, total live weight of the largest known bird would have been at least 12.33 kg.

It should be noted that a conservative profile was used for the pectoral muscle, and therefore the mass of pectoral muscle calculated from the model was only 746 g, as against the 2+ kg predicted from the relationship derived by Greenewalt (1962). An extra 2-3 cm of pectoral muscle thickness and its extension to cover the ventral third of true ribs 3 and 4, as in *Vultur gryphus* (Fisher 1946), would have resulted in 0.75 - 1.25 kg more muscle and would not have distorted the model.

12.3.4.2 *Allometric relationships* Predictions of live weight for Haast's Eagle are shown in Fig. 12.17 and Table 12.1. The relationship given by Prange *et al.* (1979) for humerus length and body mass gave a body mass of 3.99 kg for a 220 mm humerus (in the mid-range for this element). The body weight corresponding to a femur length of 154 mm (at the low end of the size distribution) was 12.81 kg (based on Prange *et al.* (1979), or 9.66 kg, and 9.47 kg if the relationships given by Alexander (1983), and Anderson *et al.* (1985), respectively are used.

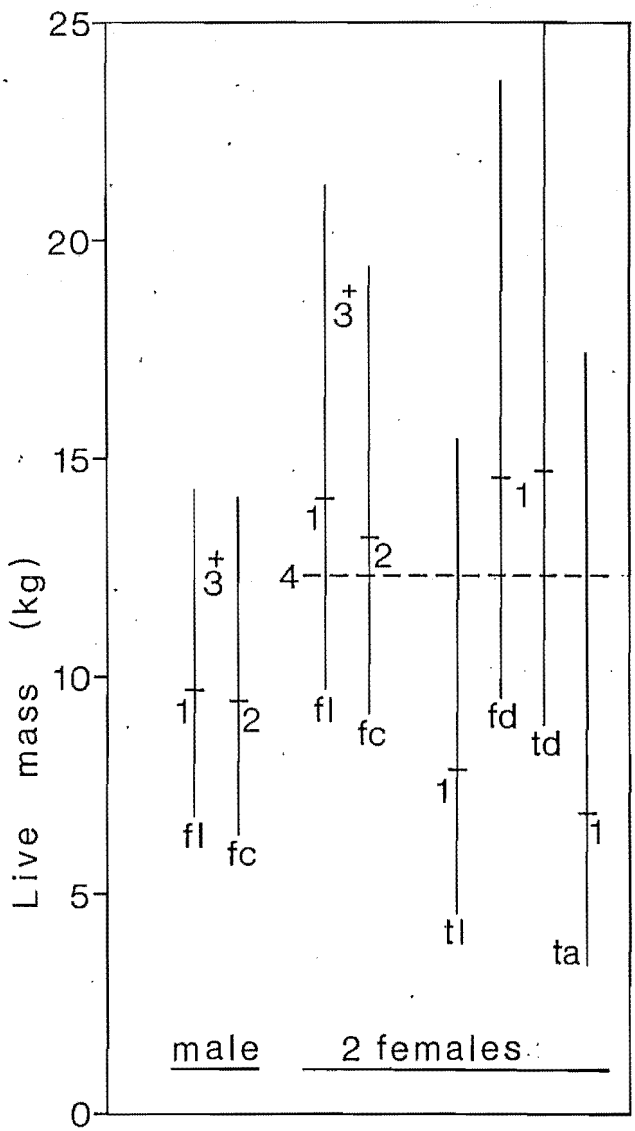

Fig. 12.17 Estimates of body weight for one male (OMNZ C 40.8) and two female (CM AV 28366; NMNZ S 22472) Haast's Eagles from allometric relationship's (with 95% confidence limits where available), and from displacement model. 1, Alexander (1983), model II; 2, Anderson *et al.* (1985); 3, Prange *et al.* (1979), femur length; 4, displacement model of female (possibly 0.5-1 kg light) - see Fig. 12.1). Estimates based on: fl, femur length; fc, femur circumference at mid-point; tl, tibiotarsus length; fd, femur mid-point sagittal diameter; td, tibiotarsus mid-point sagittal diameter; ta, tarsometatarsus length.

Table 12.1 Predicted weights (kg) of Haast's Eagle and five living species of large accipitrids in comparison with ranges in measured live weights. ELW, estimated live weight from allometric relationships based on bone dimensions given; LW, measured weights of living birds; P, from Prange *et al.* (1979); A M II, from equations using Model II regression in Alexander (1983); FL, femur length; TL, tibiotarsus length; FD, femur mid-point sagittal diameter; TD, tibiotarsus mid-point sagittal diameter; HL, humerus length.

	ELW						LW
	P	A M II					
Species	FL	FL	TL	FD	TD	HL	
Aquila audax	4.66	6.22	4.79	2.75	3.95	3.09	2.5-4.5
Harpia harpyja	8.17	6.24					4.0-9.0
Pithecophaga jefferyi	7.99	6.11					4.65
Haliaeetus leucocephalus	4.62	3.59	1.85	3.67	2.56	1.13	4.0-4.6
Harpagornis moorei ♂	11.9	8.99	4.89	9.63	7.27	4.66	
♀	18.3	13.6	7.85	14.5	14.7	6.8	
Gyps fulvus	9.49	7.22	4.41	9.36	7.42	2.87	6.9-11.0

Source for live weights: Brown & Amadon (1968).

12.3.5 Claw size

Lengths, depths, and length-depth ratios for ungual phalanges of selected large accipitrids are given in Table 12.2; dimensions used are illustrated in Fig. 12.18, with claws from several taxa of large accipitrids. These show that Haast's Eagle had the longest and deepest claws of any of these birds, which include the largest known living and extinct accipitrids. Length, depth, and depth-length ratios were consistently higher in actively predatory taxa than in known scavengers. in this respect, Haast's Eagle grouped clearly with the most active and powerful predators.

12.4 DISCUSSION

My results do not support the hypotheses that Haast's Eagle was a poor flier and a carrion feeder. Haast's Eagle had body proportions normal for an accipitrid of its size, and the wing and leg proportions were also normal. The proportions of Haast's Eagle were found to be within the range of a group that includes the large forest eagles, such as the Harpy which is known to fly through tall forest with great speed and agility (Fowler & Cope 1964; Rettig 1978). They were not similar to those of the large carrion-eating accipitrid vultures, a group that formed a distinct and separate cluster, for example, in the PCA plot of body dimensions.

An apparent dichotomy in the proportions of the major wing element lengths of accipitrids appears to be associated with different modes of flight rather than a trend towards flightlessness. Engels (1941) pointed out that the intermembral proportions of the wing skeleton in birds are not infallible indices to flight habits, except for extreme patterns. The bone proportions in the wings of Haast's Eagle may be one of these extreme patterns. The proportionately shorter ulna in Haast's Eagle may be an adaptation to flight at high weights in a structurally complex environment, because the larger forest eagles also have shorter ulnas than similar-sized open country species.

My results also suggest that Haast's Eagle flapped rather than glided, and some evidence from the Discriminant Function analysis indicated that the sexes

Table 12.2 Lengths and depths (mm) of ungual phalanges for various species of the largest accipitrids, living and extinct. FD, depth at flexor tendon boss; Ratio, ratio of length (chord of claw) to depth of flexor boss; basal claw depth.

Species	Length	FD	Ratio	BCD
Harpagornis moorei	61.5	32.4	1.90	14.4
	49.0	26.6	1.84	
	59.3	31.3	1.89	14.0
Harpia harpyja	54.4	24.4	2.43	11.6
	61.2	29.8	2.05	12.9
	55.9	25.2	2.18	11.3
Pithecophaga jefferyi	47.9	21.0	2.27	7.9
	49.6	23.1	2.15	10.4
Stephanoaetus coronatus	47.4	23.4	2.03	11.5
[1]*Titanohierax borrasi*	c57	c26	2.19	
Gyps fulvus	33.1	13.8	2.40	7.1
	27.8	11.6	2.42	6.5
Aegypius cinereus	34.0	15.0	2.27	

[1]Arredondo (1976), as *Aquila borrasi*. Transferred to *Titanohierax* by Olson & Hilgartner (1982).

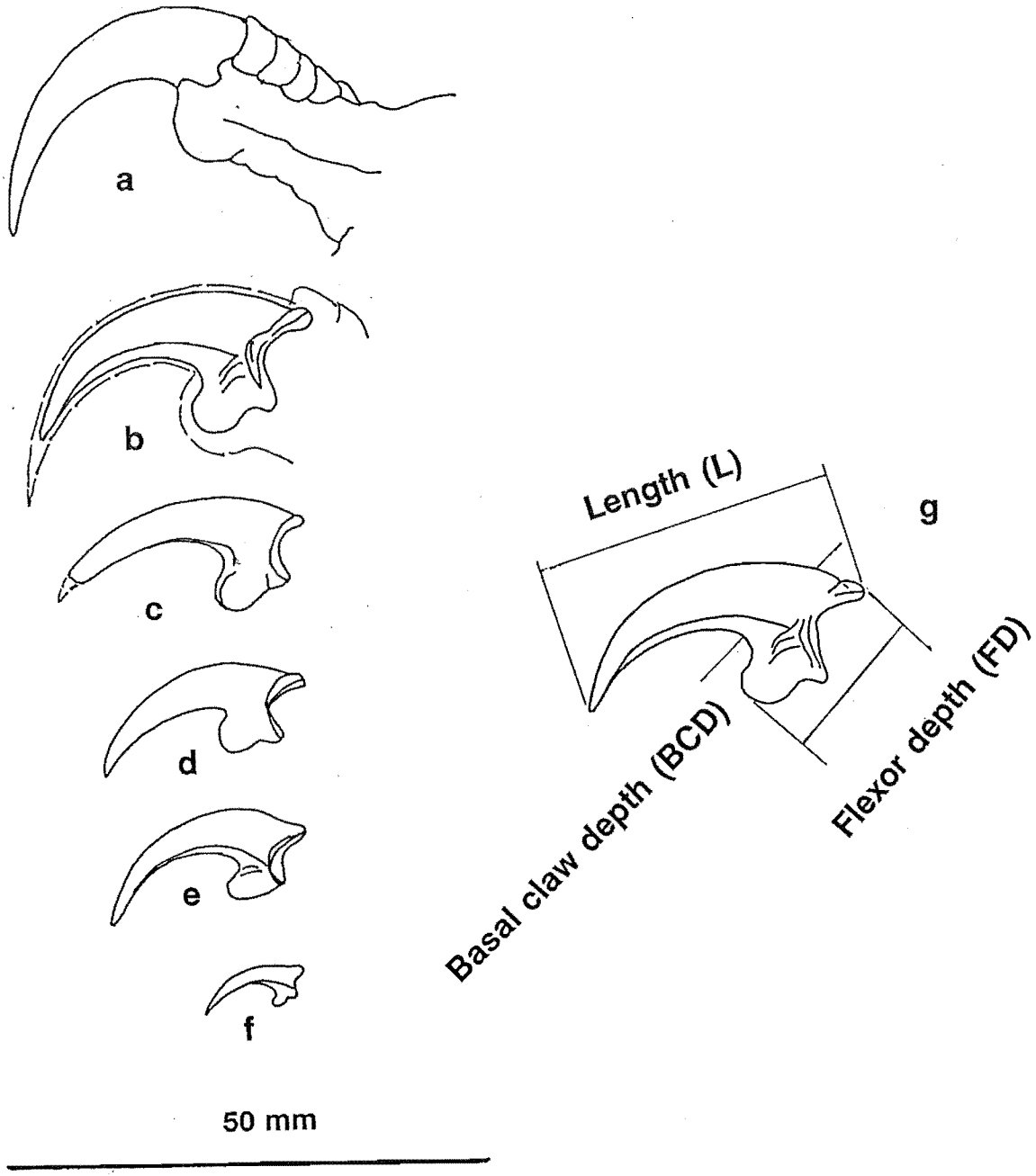

Fig. 12.18 Left lateral views of first (rear) digit ungual phalanges of large accipitrids: a, *Harpia harpyja*; b, *Harpagornis moorei*; c, *Aquila* [*Titanohierax*] *borrasi*; d, *Pithecophaga jefferyi*; e, *Aquila audax*; f, *Circus approximans*; g, diagram showing measurement landmarks used in this study.

had somewhat different proportions, and therefore, perhaps, different habits. The distal sections of the leg were more robust in the larger (presumed female) bird, and may have allowed it to take larger prey.

The carrion eating hypothesis is not supported by the presence of large claws, a feature which helped separate Haast's Eagle from the vultures in the Principal Component analysis. Goslow (1972) pointed out that the force at the point of each claw is directly related to the depth of the flexor tendon attachment boss. This dimension is larger in Haast's Eagle than in any other raptor, living or extinct (Table 12.2, Fig. 12.18) and therefore indicates that the feet and claws were capable of a powerful grip.

The base of the claw itself is also deeper in Haast's Eagle than in other species (Table 12.2), so the claw could resist greater bending loads. This may imply that the claws and toes were subjected to greater loads when catching prey than are those of living eagles, if there is a direct association between morphology and function (Reif 1983). A direct association is likely because of the close correlation between foot strength and prey size found by Voous (1969). In terms of its current fitness (Fisher 1985) - if current can be used to describe a property of an extinct bird - the long, deep claws of Haast's may be interpreted as an adaptation to the capture and killing of large prey that was capable of putting up a considerable struggle.

Voous (1969) used total claw length as an indication of predatory potential. Although total claw length includes a variable amount of horny claw over the bony core, total length of ungual phalanges alone on the Mount Owen specimen, at 372.4 mm for both feet combined, is greater than that for Harpies. The full functional claw length in Haast's Eagle would therefore have been the largest of any raptorial bird. The presence of such claws is inconsistent with an hypothesis of obligate carrion feeding.

The complete set of pedal phalanges from the Mount Owen specimen, when reassembled, gives some idea of the size and strength of the toes and claws of Haast's Eagle. Fig. 12.19 shows a dorsal view of the right foot, in comparison with an outline of the toes and claws of an Australasian Harrier (*Circus approximans*). The first (hind) and second toes have particularly thick phalanges,

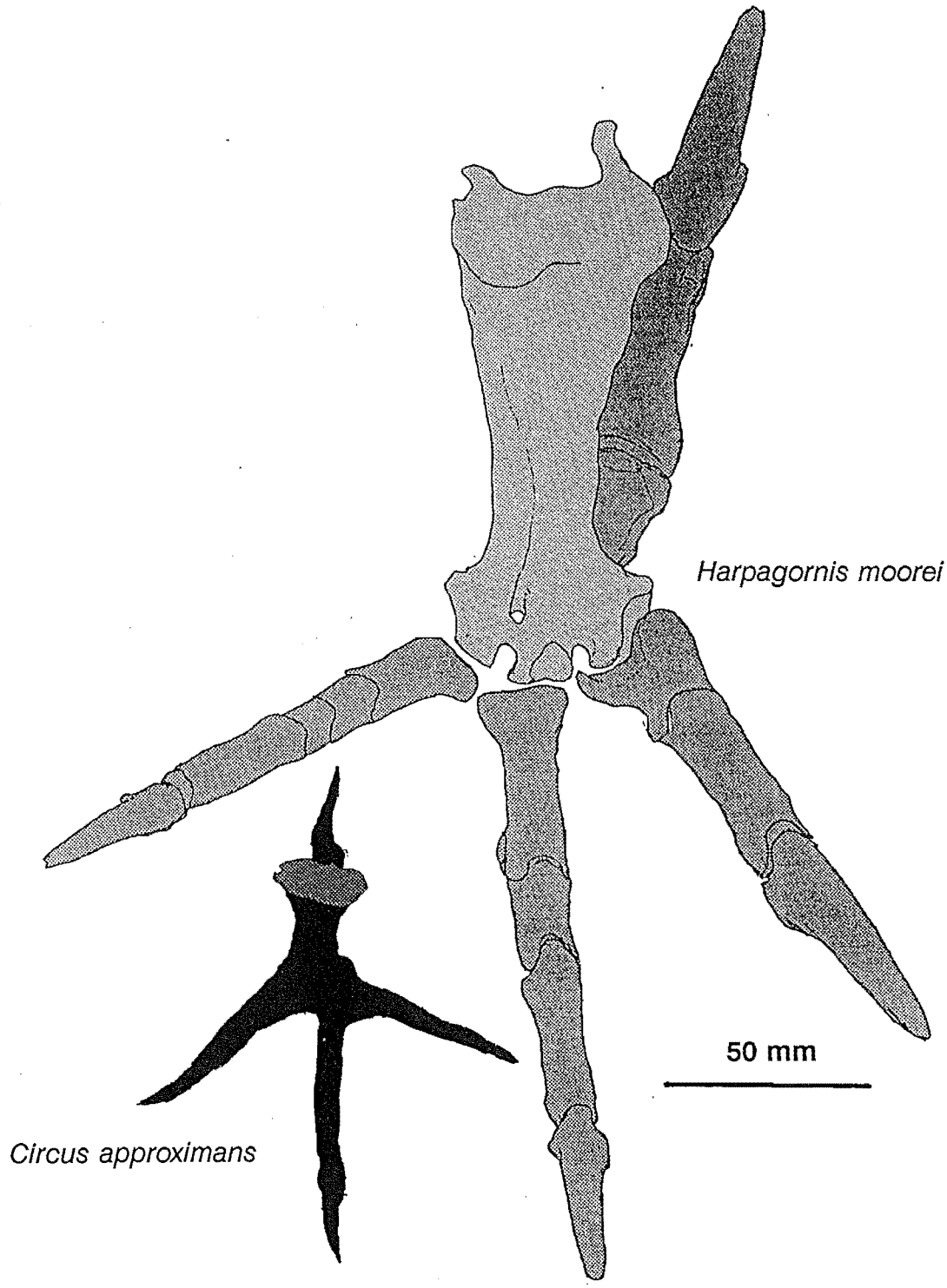

Fig. 12.19 Proximal view of re-articulated bones of right foot of *Harpagornis moorei* (specimen S 27773, Mount Owen), in comparison with whole dried foot of Australian Harrier (*Circus approximans*), to same scale. Scale bar = 50 mm.

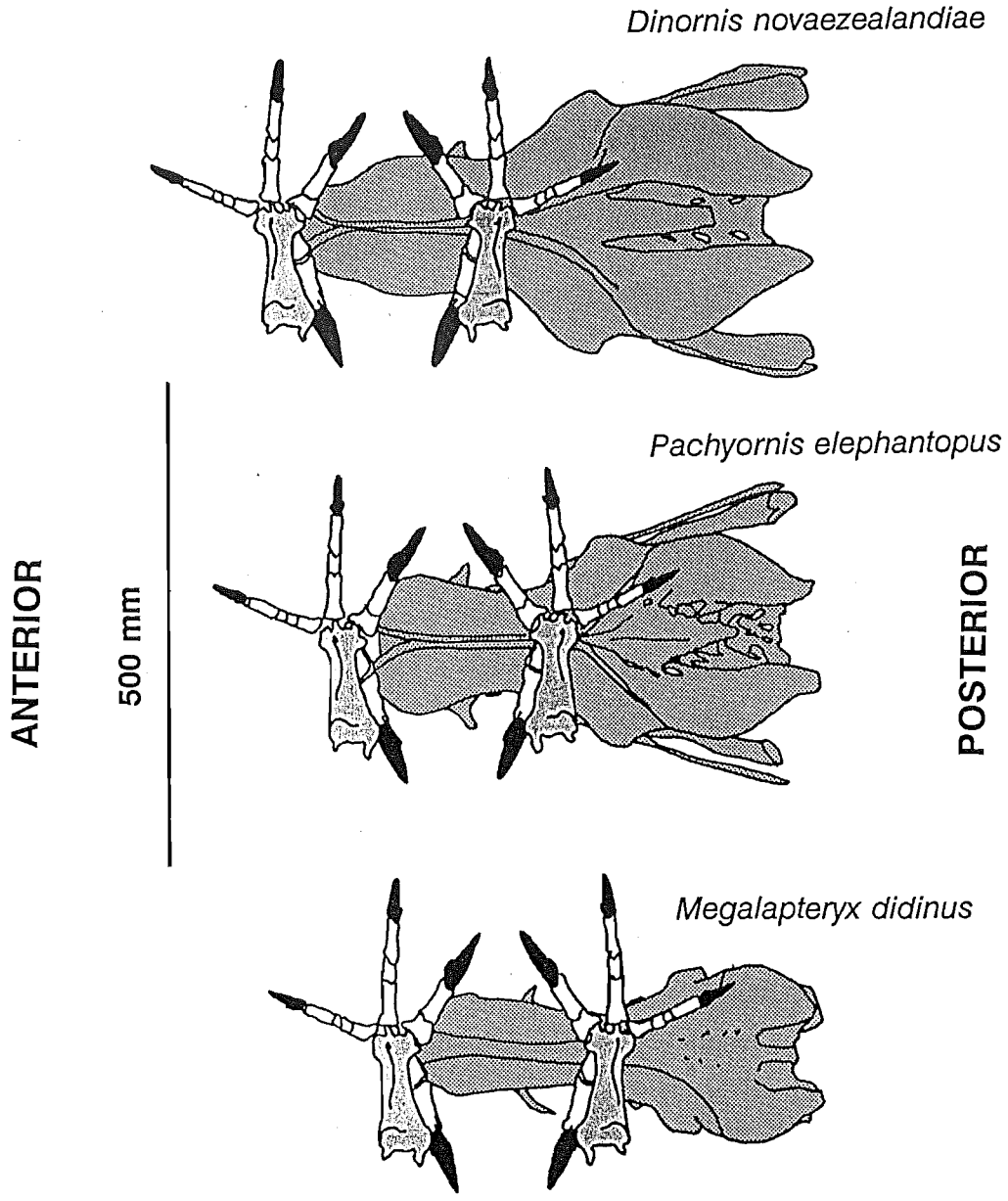

Fig. 12.20 Dorsal view of re-articulated bones of both feet of *Harpagornis moorei* (specimen S 27773, Mount Owen), in comparison with dorsal views of pelves of: (top) *Dinornis novaezealandiae*; (centre) *Pachyornis elephantopus*; (bottom) *Megalapteryx didinus*.

and the opposed claws of these total nearly 120 mm in length, without their sheaths. The predation potential of the feet is shown vividly by a comparison of the spread of both feet with the pelves of three moas (*Megalapteryx didinus, Pachyornis elephantopus, Dinornis novaezealandiae*: Dinornithiformes) (Fig. 12.20).

The hunting and feeding habits of the African Crowned Eagle (*Stephanoaetus coronatus*), which has thick strong claws and wings of similar proportions to those of Haast's Eagle, may give some clue to the habits of Haast's Eagle. The Crowned Eagle preys more on large terrestrial vertebrates than any other living eagle. It is known to kill half-grown antelopes weighing up to 18-20 kg, about five times its own weight (3.2-4.1 kg) (Brown 1982). Brown (1982) also reports that large prey require a struggle to subdue and that the eagle dismembers the body and caches limbs in trees, feeding on them over several days. "Pairs feed on each other's kills, [and are] usually present together at the site of a large kill. [The bird] will come to struggling animals caught in snares, or in [the] evening may perch close to waterholes waiting for antelopes to come to drink" (Brown 1982: 431).

The morphometric analysis suggests that Haast's Eagle was similar in conformation and flight mode to the largest of the predatory forest eagles. The presence of its bones in caves (where it would have been attracted to struggling prey), and in swamps and near pools and lakes suggest that it may have hunted its prey in similar ways and in similar places to those used by the Crowned Eagle.

In one respect, however, Haast's Eagle is reminiscent of large carrion feeders. It had a beak that was more like that of a vulture than of an eagle. The long, narrow beak (see Chapter 2) is similar to those of *Gyps* vultures, which feed in the depths of large carcases. Bill length has increased in Haast's Eagle at the expense of a larger bony nostril opening, and Haast's Eagle is unique among the large eagles in always having a bone scroll surrounding the nostril (Plate 3, Chapter 2). The bony protection for the nostril seems to be analogous to the bony plate covering much of the external nares in the accipitrid vultures

(Chapter 2), and it may be an adaptation that reduces the likelihood of damage to the nostril area while the bill is deep inside a carcase. Other eagles pull at the exterior of a carcase, and do not immerse the bill and head in the prey's body cavity.

A longer, more slender bill, with protection for the nostril simply means that Haast's Eagle could deal with large prey items and does not itself support the carrion feeding hypothesis. Vultures have weak hind limbs and short claws. The morphology of the hind limbs clearly indicates that the eagle could and did attack and kill prey several times larger than itself.

12.4.1 Conclusions

The results of my ecomorphological analysis support the conclusions of the chapters on habitat and associated species. Haast's Eagle was a predator. It used flapping flight, rather than gliding, which also supports the active predator model, because carrion feeders and other birds that rely on dispersed food soources always glide or soar (Pennycuick 1972). The size and morphology of its hind limbs and feet allowed it to hunt and kill the largest available prey, which in New Zealand was the large flightless ground birds.

An unexpected result was that the two sexes were apparently different in their locomotory and predatory potential. This may indicate that the sexes took different prey.

Although phylogenetically near a group of open country eagles, Haast's Eagle was closer in its functional morphology to the largest forest eagles. Its flight pattern and hunting techniques were probably similar to those taxa rather than to its nearest relatives. In bill form, Haast's eagle is convergent on the accipitrid vultures.

Taken together, the mosaic of features demonstrates clearly the functional morphological plasticity of the accipitrids that has obscured the phylogenetic relationships within the group. There was apparently sufficient range of variance in pre-existing structures within the ancestral population that gave rise to Haast's Eagle, to allow it to converge on two different trophic and locomotory groups at the same time, to exploit a supply of large prey in a mammal-free environment.

APPENDICES: CHAPTER 5: Measurements of accipitrid skeletons; see Table 5.1 for specimens.

See Fig. 4.1 for measurement landmarks, and explanation of abbreviations.

APPENDIX 12.1 48 genera: femur, cranium, and premaxilla

Measurements (mm) of femora, cranium, and premaxilla. L, length; P, proximal width; Ms, sagittal midshaft diameter; Mm, medial midshaft diameter; D, distal width; POw, postorbital width.

Femur						Cranium			Premaxilla		
Genus	L	P	Ms	Mm	D	L	D	POw	L	D	W
PANDION	77.8	16.6	7.4	7.5	16.5	82.9	33.5	42.7	40.1	14.4	20.9
SAGITTAR	109.4	27.3	13.6	13.0	26.3	114.8	41.9	56.0	56.4	20.0	25.0
AVICEDA	42.7	9.2	3.9	4.0	9.5	61.8	27.9	35.7	23.6	12.5	15.9
LEPTODON	-	-	-	-	-	-	-	-	-	-	-
ELANOIDE	45.2	9.4	4.4	4.8	9.5	62.9	28.5	38.0	26.5	10.5	13.8
PERNIS	54.2	13.1	6.0	6.6	12.9	77.4	33.7	41.0+	31.0	12.1	17.4
MACHAERH	66.9	13.8	6.6	6.4	13.6	79.9	31.5	42.9	36.8	11.7	18.5
ELANUS	48.7	9.2	4.2	4.3	9.6	55.6	23.9	32.1	20.1	9.2	13.9
CHELICTI	-	-	-	-	-	-	-	-	-	-	-
ICTINIA	43.9	9.0	4.2	4.3	9.1	53.8	25.4	33.0	20.9	9.9	13.9
MILVUS	71.1	14.2	6.7	7.2	13.6	82.0	32.7	43.9	35.1	14.9	18.1
HALIASTU	52.3	10.9	5.2	5.6	11.5	65.3	29.2	37.3	27.6	12.7	14.9
HALIAAET	117.5	26.2	11.3	12.2	27.3	126.5	45.5	63.6	59.8	26.1	29.8
2						109.5	40.6	53.6	51.7	22.9	23.2
ICHTHYOP	104.3	21.3	10.3	10.5	24.0	101.3	36.8	51.2	44.7	21.4	21.2
ICHTHYO2	79.0	16.3	8.0	8.3	18.3	83.3	33.2	42.9	37.8	16.0	18.1
GYPOHIER	75.0	16.2	7.2	7.7	16.6	101.0	36.5	44.9	50.2	14.0	14.7
NEOPHRON	75.7	19.9	7.7	8.4	17.7	101.7	39.7	47.9	51.8	13.8	15.6
GYPAETUS	120.8	27.5	13.1	12.7	29.1	145.5	45.7	66.6	72.3	22.9	30.0
NECROSYR	81.8	19.1	8.5	9.2	19.6	100.7	37.9	46.5	53.1	12.5	19.3
GYPS	118.2	29.6	12.5	12.6	26.4	125.5	42.6	48.9	62.2	20.0	24.1
AEGYPIUS	137.9	37.6	16.9	16.9	37.8	156.3	53.4	82.0	80.6	32.0	38.7
CIRCAETU	81.4	17.2	8.3	8.7	17.2	103.7	41.8	67.9	40.6	20.6	22.7
TERATHOP	89.1	20.4	9.1	9.4	20.9	113.0	47.4	63.7	42.4	23.5	23.5
SPILORNI	77.8	17.9	8.9	9.1	19.9	91.7	36.6	52.6	38.8	17.4	19.8
POLYBORO	82.9	12.5	6.3	6.2	12.3	71.6	31.7	36.2	30.7	13.1	13.2
CIRCUS	74.6	13.1	6.1	6.4	13.6	71.0	30.5	40.8	32.6	15.5	15.6
MELIERAX	43.8	7.9	3.4	3.4	7.8	45.1	22.0	26.2	15.4	9.4	10.0
ERYTHROT	-	-	-	-	-	-	-	-	-	-	-
ACCIPITE	54.3	9.5	4.4	4.6	10.1	50.6	23.5	28.7	19.2	10.4	12.3
BUTASTUR	-	-	-	-	-	67.0	28.6	36.5	26.3	11.5	15.2
KAUPIFAL	53.3	9.8	4.6	4.5	10.2	58.6	25.4	35.8	22.3	10.9	13.3
LEUCOPTE	58.6	11.2	5.1	5.3	12.1	67.6	27.8	38.6	25.6	13.5	15.5
BUTEOGAL	89.6	19.2	9.0	8.7	18.7	95.8	36.8	52.5	42.9	18.7	19.9
HETEROSP	77.1	14.8	7.6	7.5	16.5	80.7	33.7	46.3	33.5	15.3	18.3
BUSARELL	84.5	15.7	7.0	7.7	16.4	84.4	34.8	45.4	38.4	15.1	16.1
GERANOAE	97.9	18.4	9.3	8.7	20.3	103.1	40.0	56.9	43.0	18.1	23.9
BUTEO	76.7	14.9	6.8	6.8	15.7	77.8	33.5	45.0	32.4	14.4	17.1
PARABUTE	74.5	14.3	6.2	6.4	15.3	74.5	31.5	42.2	28.5	15.2	16.7
MORPHNUS	91.8	18.9	8.6	8.9	19.5	92.6	39.4	54.8	37.0	19.2	17.9
						84.8	37.1	52.9	30.2	18.2	16.3
						84.4	33.4	47.8	34.3	17.1	16.4

APPENDIX 12.1 continued

Measurements (mm) of femora, cranium, and premaxilla. L, length; P, proximal width; Ms, sagittal midshaft diameter; Mm, medial midshaft diameter; D, distal width; POw, postorbital width.

	Femur					Cranium			Premaxilla		
Genus	L	P	Ms	Mm	D	L	D	POW	L	D	W
HARPIA	119.9	31.2	15.5	15.4	34.2	125.1	46.5	65.3	56.2	28.5	27.1
Remeasured						125.0	47.6	65.5	56.0	28.5	26.1
						109.3	41.9	59.4	49.0	24.4	24.9
						127.2	47.9	67.4	55.8	30.6	29.0
						112.3	41.9	57.4	46.9	25.8	24.2
PITHECOP	122.2	29.0	12.7	13.8	31.2	135.8	48.7	71.4	67.3	38.1	25.8
						136.3	48.9	70.4	62.2	39.2	26.5
						137.0	47.9	72.8	64.0	39.3	26.0
ICTINAET	-	-	-	-	-	-	-	-	-	-	-
AQUILA1	126.8	29.4	12.6	12.9	30.4	115.1	44.6	63.4	48.4	22.7	27.5
						116.2	47.9	63.6	49.5	22.5	26.5
						117.7	45.2	63.6	49.5	21.2	25.6
						107.1	43.4	63.3	44.5	20.5	24.1
						116.1	49.1	64.1	50.5	22.8	25.5
AQUILA2						123.0	43.8	62.1	55.8	24.0	26.5
						123.6	45.2	64.1	53.4	24.1	26.3
						115.9	45.0	62.2	52.2	22.6	26.4
						127.4	45.0	64.8	57.2	24.0	25.5
HIERAAET	92.5	18.9	8.3	8.8	19.3	92.0	38.3	50.9	34.7	17.2	18.7
LOPHOAET	83.8	16.6	8.1	7.9	17.3	95.3	34.7	51.9	39.0	16.1	20.5
						95.3	38.6	53.0	39.4	16.2	19.2
						92.9	36.4	52.8	38.3	16.9	18.8
						91.5	37.1	52.5	38.3	16.5	18.3
SPIZAETU	79.9	16.8	7.9	7.8	17.7						
STEPHANO	108.0	24.9	11.8	11.9	25.8	102.6	41.7	56.4	42.3	21.8	56.4
						108.4	42.0	58.5	46.5	24.8	24.1
POLEMAET	121.5	26.8	12.2	13.0	26.8	114.7	43.4	69.0	48.0	22.5	25.3
						116.8	43.9	66.3	48.5	22.9	22.5
						123.0	45.9	70.1	51.1	23.9	23.6
						118.1	46.2	69.4	46.4	24.5	23.4
						122.0	45.5	70.5	50.9	23.7	22.7
						120.5	48.3	67.7	52.7	22.5	26.0
GERANOSP	71.1	9.7	4.5	4.4	9.2	58.4	25.9	33.0	21.6	11.4	12.2
HARPAGUS	44.8	8.6	4.0	4.1	9.4	50.1	25.7	33.1	19.1	10.9	13.3
CHONDROH	45.3	9.7	4.3	4.4	8.9	65.0	27.9	30.6	27.4	12.1	15.1
ROSTRHAM	52.0	9.4	4.9	5.1	10.0	64.0	28.2	34.0	27.6	9.0	13.1
GAMPSONY	36.6	6.7	3.0	3.0	7.1	40.2	17.3	22.3	15.0	6.6	10.1
SPIZASTU	77.6	17.3	7.3	7.6	18.5	79.8	33.0	47.1	30.6	16.1	16.8
UROTRIOR	74.5	15.1	6.8	6.8	15.9	68.7	30.3	40.2	25.0	15.2	15.8

APPENDIX 12.2 48 genera: tibiotarsus

Measurements (mm) of tibiotarsus of 48 genera of Accipitridae. Abbreviations as in Appendix 5.1, except Pfib, distance from proximal extremity of inner cnemial crest to distal end of fibular crest.

Tibiotarsus

Genus	L	P	Ms	Mm	D	Pfib
SAGITTAR	268.4	31.8	9.6	11.6	20.1	60.1
PANDION	127.1	18.9	7.0	7.2	15.4	53.0
AVICEDA	63.3	9.5	3.0	3.6	8.3	26.8
ELANOIDE	62.5	11.0	3.7	3.9	9.2	23.5
PERNIS	83.9	13.6	4.6	5.8	11.3	31.0
MACHAERH	97.0	14.1	4.8	5.2	10.9	34.5
ELANUS	61.6	9.3	3.7	4.1	9.1	23.8
CHELICTI	-	-	2.6	2.5	6.4	-
ICTINIA	62.6	9.4	3.0	3.5	7.7	22.8
MILVUS	92.5	14.6	5.1	5.6	11.8	35.1
HALIASTU	73.7	11.5	3.7	4.5	9.5	27.6
HALIAAET	156.7	26.4	7.8	10.2	19.6	59.6
ICHTHYO1	160.8	22.7	8.0	9.6	18.9	60.7
GYPOHIER	119.3	18.2	5.7	6.7	14.2	46.1
NEOPHRON	123.2	19.6	6.8	7.6	14.5	45.7
GYPAETUS	171.8	31.0	9.1	11.2	21.3	64.5
NECROSYR	126.3	20.5	7.2	7.9	14.7	43.8
GYPS	166.3	28.1	9.1	10.4	20.7	62.6
AEGYPIUS	216.5	38.0	11.6	13.6	26.2	81.3
CIRCAETU	126.8	17.6	6.4	7.6	14.2	44.6
TERATHOP	132.4	20.9	7.0	8.5	17.0	49.3
SPILORNI	129.1	19.4	6.9	7.8	15.2	46.2
POLYBORO	117.2	13.5	5.1	5.0	8.5	41.5
CIRCUS	114.4	13.7	4.7	5.6	10.4	37.5
MELIERAX	63.0	8.1	2.7	3.1	6.5	23.0
ERYTHROT	-	-	-	-	-	-
ACCIPITE	74.5	10.0	3.3	4.0	7.7	25.3
BUTASTUR	-	-	-	-	-	-
KAUPIFAL	72.6	10.3	3.8	4.2	8.8	26.6
LEUCOPTE	83.0	11.9	4.5	4.7	10.1	28.0
BUTEOGAL	149.8	20.3	6.2	7.6	15.3	48.5
HETEROSP	123.2	16.9	5.2	6.2	13.1	39.0
BUSARELL	125.0	17.0	5.7	6.7	13.8	42.5
GERANOAE	135.7	20.5	6.7	7.9	16.4	50.0
BUTEO	105.4	15.6	5.3	6.4	12.1	36.3
PARABUTE	106.0	15.0	4.8	5.9	11.4	34.4
MORPHNUS	-	-	-	-	-	-
HARPIA	183.2	34.9	10.8	12.7	27.6	73.7
PITHECOP	200.0	30.4	10.2	11.4	22.5	71.3
ICTINAET						
AQUILA	169.8	31.0	9.3	11.5	22.9	68.1
HIERAAET	132.6	18.9	6.0	7.8	14.5	48.6
LOPHOAET	120.7	17.2	5.9	7.0	13.4	43.9
SPIZAETU	114.2	16.9	5.6	6.9	13.4	40.9
STEPHANO	152.2	25.2	8.5	10.2	21.3	62.8
POLEMAET	180.5	25.6	8.3	11.0	20.6	69.9
GERANOSP	106.5	10.2	3.6	4.0	7.3	32.7
GAMPSONY	48.4	8.1	2.8	2.8	6.8	18.4
CHONDROH	67.5	9.2	3.7	3.8	8.5	24.5
UROTRIOR	110.5	16.4	5.5	6.4	12.7	41.4
ROSTRHAM	76.2	10.5	3.9	4.4	8.7	28.0
HARPAGUS	64.2	9.1	3.2	3.5	7.6	21.4
SPIZASTU	114.8	18.2	5.9	6.8	13.4	43.6
HARPYHAL	154.5	23.2	7.1	9.0	18.0	53.2

APPENDIX 12.3 48 genera: mandible

Measurements (mm) of mandible of representatives of 48 genera of Accipitridae. L, length from anterior extremity of symphysis to line touching both retroarticular processes; W, maximum width across rami; SL, symphysis length; Daa, depth of ramus anterior to articular process; Dsa, depth of ramus at surangular; Tc, distance from tip to coronoid process; Tsa, distance from tip to surangular process; Ds, depth at posterior end of symphysis; Wart, width across posterior ramus and articular process.

Mandible

Genus	L	W	SL	Daa	Dsa	Tc	Tsa	Ds	War
SAGITTAR	87.6	-	14.1	6.2	8.1	69.0	63.5	6.6	17.5
PANDION	55.7	39.6	13.5	6.1	7.4	47.5	42.6	5.9	14.1
AVICEDA	39.2	27.9	7.3	3.4	5.1	34.4	32.4	4.3	10.5
LEPTODON	-	-	-	-	-	-	-	-	-
ELANOIDE	42.5	31.9	8.4	3.8	4.8	35.8	35.0	3.7	10.5
PERNIS	53.6	29.3	9.9	3.6	5.4	47.5	46.6	3.6	10.5
MACHAERH	59.9	38.8	7.4	3.7	4.5	53.6	51.7	3.6	13.0
ELANUS	35.9	31.7	4.3	2.2	3.1	32.7	29.2	2.5	9.8
CHELICTI	-	-	-	-	-	-	-	-	-
ICTINIA	35.0	27.8	6.6	2.6	5.3	30.1	28.6	3.3	10.4
MILVUS	59.0	39.2	10.6	4.1	6.2	50.1	46.9	4.7	14.3
HALIASTU	43.9	30.1	8.9	3.4	5.4	37.3	35.1	4.1	11.8
HALIAEET	96.6	62.8	20.2	7.4	11.7	83.6	77.3	8.2	24.1
HALIAEE2	82.3	50.1	16.7	-	-	-	-	-	19.0
ICHTHYO1	71.6	45.7	16.2	6.0	10.8	60.9	56.4	7.2	16.6
GYPOHIER	75.8	37.2	16.9	4.9	9.2	64.3	60.6	5.6	14.7
NEOPHRON	76.5	44.6	13.7	5.9	7.9	65.7	62.0	8.9	15.0
GYPAETUS	114.4	89.4	11.6	8.4	11.9	92.9	83.6	6.7	29.0
NECROSYR	75.2	41.6	13.6	4.8	8.2	65.9	61.4	4.9	14.1
GYPS	100.6	49.7	19.3	7.1	12.8	81.7	75.4	10.1	18.6
AEGYPIUS	122.3	81.5	25.6	10.1	16.9	103.1	95.7	11.2	30.0
CIRCAETU	77.9	51.2	12.8	5.7	8.1	68.6	62.1	5.6	18.1
TERATHOP	80.6	59.9	15.6	5.7	10.1	70.7	67.3	6.3	21.7
SPILORNI	67.1	41.2	12.8	5.0	7.8	57.1	54.7	5.5	16.1
POLYBORO	48.7	31.2	9.5	3.5	5.6	41.6	37.8	3.7	10.9
CIRCUS	51.5	34.6	9.2	3.8	5.9	44.5	41.3	3.9	12.7
MELIERAX	28.2	21.8	4.3	2.5	3.5	24.4	22.5	2.0	8.0
ERYTHROT	-	-	-	-	-	-	-	-	-
ACCIPITE	31.5	25.0	5.1	2.7	4.1	26.1	25.0	3.0	9.2
BUTASTUR	-	-	-	-	-	-	-	-	-
KAUPIFAL	41.2	26.7	7.4	2.9	4.5	35.1	34.3	3.3	10.3
LEUCOPTE	46.2	31.1	9.3	3.1	5.4	39.6	39.2	3.7	11.2
BUTEOGAL	65.5	43.0	14.5	4.5	8.2	56.0	52.3	5.2	14.4
HETEROSP	56.1	39.5	11.2	4.1	7.1	48.7	46.4	5.0	14.4
BUSARELL	56.7	38.1	11.9	4.7	6.9	48.1	45.8	5.3	15.2
GERANOAE	74.8	52.2	12.5	5.0	7.7	66.9	64.3	5.0	17.7
BUTEO	54.4	37.6	10.0	4.1	6.2	46.9	45.1	4.1	14.1
PARABUTE	51.4	35.0	9.8	3.5	5.7	43.9	41.7	4.1	12.8
MORPHNUS	65.0	40.1	12.3	5.3	7.9	55.5	51.7	5.6	-
	62.1	39.9	11.9	-	-	-	-	-	15.9
HARPIA	88.8	61.3	19.1	8.3	11.5	75.9	69.5	8.6	24.0
	79.5	52.0	17.1	-	-	-	-	-	19.8
	92.8	64.0	19.0+	-	-	-	-	-	24.5
	81.1	54.5	16.9	-	-	-	-	-	19.9

APPENDIX 12.3 continued

Measurements (mm) of mandible of representatives of 48 genera of Accipitridae. L, length from anterior extremity of symphysis to line touching both retroarticular processes; W, maximum width across rami; SL, symphysis length; Daa, depth of ramus anterior to articular process; Dsa, depth of ramus at surangular; Tc, distance from tip to coronoid process; Tsa, distance from tip to surangular process; Ds; depth at posterior end of symphysis; Wart, width across posterior ramus and articular process.

Mandible

Genus	L	W	SL	Daa	Dsa	Tc	Tsa	Ds	Wart
PITHECOP	97.4	56.6	22.6	7.8	13.6	84.1	79.0	9.5	21.4
	99.6	59.4	25.2	-	-	-	-	-	22.6
	97.5+	62.1	24.2+	-	-	-	-	-	24.1
ICTINAET	-	-	-	-	-	-	-	-	-
AQUILA1	83.5	58.7	16.1	7.7	11.4	70.7	68.2	6.6	22.0
	81.0	54.8	17.1	-	-	-	-	-	21.0
	82.8	57.0	14.8	-	-	-	-	-	21.8
	79.8	52.0	16.1	-	-	-	-	-	19.7
	83.7	56.1	16.5	-	-	-	-	-	21.1
AQUILA2	92.7	54.8	17.8	-	-	-	-	-	20.2
	91.0	57.1	18.7	-	-	-	-	-	22.7
	88.2	56.1	18.7	-	-	-	-	-	21.3
	94.4	61.4	19.8	-	-	-	-	-	21.6
HIERAAET	62.4	41.3	11.8	5.1	7.9	53.9	52.0	5.3	15.0
LOPHOAET	71.5	44.9	11.7	3.9	6.0	64.2	62.5	4.0	14.8
	70.8	46.8	13.1	-	-	-	-	-	15.5
	69.3	45.2	12.8	-	-	-	-	-	15.9
	68.8	44.6	11.1	-	-	-	-	-	15.9
SPIZAETU	55.1	36.6	10.8	4.3	6.7	47.1	44.9	3.9	13.6
	60.2	38.4	12.7	-	-	-	-	-	14.4
STEPHANO	72.7	48.6	13.1	6.5	10.4	62.7	58.8	6.4	19.0
	81.4	52.4	15.8	-	-	-	-	-	19.9
POLEMAET	83.6	53.7	16.6	6.7	10.5	72.7	69.4	6.6	20.8
	87.4	55.8	19.2	-	-	-	-	-	21.9
	88.9	57.9	17.9	-	-	-	-	-	23.6
	85.4	56.2	17.7	-	-	-	-	-	22.4
	89.2	51.6	18.3	-	-	-	-	-	22.3
	87.5	56.9	19.0	-	-	-	-	-	22.8
GERANOSP	39.6	28.7	6.5	2.6	4.0	33.5	31.3	2.8	9.9
GAMPSONY	26.4	21.3	3.8	1.8	2.7	23.2	21.6	2.2	7.3
ROSTRHAM	43.1	28.4	7.1	2.7	4.9	37.5	35.8	3.4	9.8
CHONDROH	46.7	31.6	11.3	3.4	5.6	40.5	39.9	4.2	11.4
UROTRIOR	46.6	32.4	8.6	3.5	6.3	40.2	38.1	4.0	12.5
HARPAGUS	31.3	26.3	6.7	2.8	5.0	27.5	26.3	3.4	9.8
SPIZASTU	53.8	38.4	10.6	4.8	7.1	47.2	46.9	4.6	14.1

APPENDIX 12.4 18 genera: tarsometatarsus

Measurements (mm) of tarsometarsus of representatives of 18 genera of Accipitridae. L, total length; P, proximal width; Ms, sagittal midshaft diameter; Mm, midshaft medial diameter; Dl, distal width; Dap, distal cranio-caudal depth.

Tarsometatarsus

Genus	L	P	Ms	Mm	Dl	Dap
ELANOIDE	33.8	8.9	2.9	4.7	9.5	5.2
MILVUS	59.4	11.9	5.6	6.3	13.5	8.2
HALIASTU	47.8	10.1	4.4	5.0	11.1	5.8
NEOPHRON	78.6	15.6	6.5	7.5	16.9	10.2
CIRCAETU	90.0	14.8	7.4	7.4	15.0	9.0
POLYBORO	80.6	9.1	4.0	6.7	7.6	5.8
MELIERAX	46.0	6.7	3.1	3.1	7.2	4.4
ACCIPITE	61.9	7.8	3.3	3.0	8.0	4.6
KAUPIFAL	50.3	8.6	4.1	4.8	9.4	6.3
LEUCOPTE	62.3	10.4	5.3	5.5	11.5	7.2
HETEROSP	104.5	13.5	6.3	6.8	15.2	8.2
BUSARELL	88.9	14.1	7.0	7.3	17.1	9.7
PITHECOP	122.0	23.4	13.8	15.7	26.8	15.6
SPIZAETU	81.8	13.9	7.4	7.9	15.9	10.0
GERANOSP	79.7	7.6	3.3	5.2	7.2	4.3
HARPAGUS	44.0	8.1	3.3	3.9	7.7	4.7
HARPYHAL	120.4	18.5	9.7	10.0	22.0	10.8
UROTRIOR	78.5	12.7	7.0	6.6	13.6	8.2

APPENDIX 12.5

Dimensions (mm) of eagles in British Museum (Natural History) and National Museum of Natural History, Smithsonian Institution.

A. Cranium

Genus	Cat no.	L	PrL	CrD	PrD	PoW	PrW	NL	ND	IOw
HARPIA	1872.10.25.1	109.3	49.0	41.9	24.4	59.4	24.9	15.5	11.8	23.6
	1862.3.19.14	127.2	55.8	47.9	30.6	67.4	29.0	18.4	16.0	29.4
	1862.3.14.19	112.3	46.9	41.9	25.8	57.4	24.2	13.8	12.0	23.0
	429223	125.0	56.0	47.6	28.5	65.5	26.1	19.1	11.7	30.9
PITHEC	1961.23.1	136.3	62.2	48.9	39.2	70.4	26.5	21.7	17.2	34.2
	1910.2.11.1A	137.0	64.0	47.9	39.3	72.8	26.0	21.5	18.3	38.0
POLEMA	1952.1.179	116.8	48.5	43.9	22.9	66.3	22.5	14.3	10.1	26.7
	1853.10.21.1	123.0	51.1	45.9	23.9	70.1	23.6	17.0	11.1	26.2
	1957.9.1	118.1	46.4	46.2	24.5	69.4	23.4	15.9	12.2	27.6
	1954.30.43	122.0	50.9	45.5	23.7	70.5	22.7	15.4	12.2	28.1
	1984.101.1	120.5	52.7	48.3	22.5	67.7	26.0	14.6	10.7	25.8
STEPHANO	1954.30.42	108.4	46.5	42.0	24.8	58.5	24.1	13.4	9.9	24.6
SPIZAETU	1952.1.177	84.4	34.3	33.4	17.1	47.8	16.4	11.7	7.7	19.2
	430495	79.6	29.4	33.5	16.4	46.7	16.5	10.2	6.5	17.6
MORPHNUS	1851.12.2.10	84.8	30.2	37.1	18.2	52.9	16.3	10.6	8.2	18.7
LOPHOAET	1861.1.19.6	95.3	39.4	38.6	16.2	53.0	19.2	12.0	6.9	18.5
	1861.1.19.4	92.9	38.3	36.4	16.9	52.8	18.8	12.2	7.0	19.1
	1954.30.41	91.5	38.3	37.1	16.5	52.5	18.3	12.1	7.1	16.2
AQUILA1	1869.12.22.10	116.2	49.5	47.9	22.5	63.6	26.5	14.7	10.3	25.7
	1973.66.57	117.7	49.5	45.2	21.2	63.6	25.6	15.2	10.5	25.8
	1858.5.4.444	107.1	44.5	43.4	20.5	63.3	24.1	14.6	10.5	25.2
	1922.3.24.260	116.1	50.5	49.1	22.8	64.1	25.5	16.3	11.7	25.3
AQUILA2	1966.51.16	123.0	55.8	43.8	24.0	62.1	26.5	15.1	12.2	27.2
	1898.5.7.6	123.6	53.4	45.2	24.1	64.1	26.3	14.9	10.7	30.1
	1930.3.24.258	115.9	52.2	45.0	22.6	62.2	26.4	15.0	12.1	25.3
	1954.30.50	127.4	57.2	45.0	24.0	64.8	25.5	16.1	11.9	26.9
HALIAEE	1856.9.28.1	109.5	51.7	40.6	22.9	53.6	23.2	13.9	10.0	23.4

B Mandible, sternum

	Mandible				Sternum						
Genus	L	W	SL	Wart	L	Wsc	Wp	D	Dant	Lcar	Dac
HARPIA	79.5	52.0	17.1	19.8	117.3	54.3	58.1	54.7	38.6	95.8	33.7
	92.8	64.0	19.0	24.5	135.4	65.3	-	65.2	48.8	95.7	38.1
	81.1	54.5	16.9	19.9	124.5	58.2	61.2	55.6	40.0	102.0	32.6
	88.8	61.2	19.1	24.0	137.4	65.3	79.3	64.7	49.7	107.8	37.7
PITHECOP	99.6	59.4	25.2	22.6	123.5	66.4	71.4	54.4	39.7	86.1	34.6
	97.5	62.1	24.2	24.1	129.5	68.2	79.3	59.0	41.8	99.5	38.4
POLEMAET	87.4	55.8	19.2	21.9	118.9	71.9	72.1	60.0	46.0	92.9	42.1
	88.9	57.9	17.9	23.6	120.7	67.8	72.9	60.6	46.3	103.2	-
	85.4	56.2	17.7	22.4	120.1	60.7	69.6	57.6	43.6	93.7	39.3
	89.2	51.6	18.3	22.3	-	-	-	-	-	-	-
	87.5	56.9	19.0	22.8	125.5	69.6	76.4	59.7	48.2	96.5	39.0
STEPHANO	81.4	52.4	15.8	19.9	115.9	60.3	68.7	55.0	39.1	100.8	35.8
	-	-	-	-	110.5	59.0	61.6	53.7	41.8	97.8	33.0
SPIZAETU	60.2	38.4	12.7	14.4	74.3	37.6	45.0	37.1	27.2	64.8	24.5
	55.1	36.4	11.5	13.6	71.2	34.6	42.0	32.4	25.4	62.2	25.4
MORPHNUS	62.1	39.9	11.9	15.9	79.8	42.8	43.6	39.0	28.6	63.8	20.6
LOPHOAET	70.8	46.8	13.1	15.5	71.3	38.5	43.6	36.0	27.2	60.7	22.1
	69.3	45.2	12.8	15.9	72.1	41.6	44.5	35.0	28.0	59.4	23.6
	68.8	44.6	11.1	15.9	72.6	40.6	46.6	35.5	24.1	58.1	23.8
	-	-	-	-	71.5	38.3	43.3	34.3	27.3	61.4	23.8
AQUILA1	81.0	54.8	17.1	21.0	111.1	61.6	64.2	46.3	35.7	90.0	31.2
	82.8	57.0	14.8	21.8	120.0	65.3	75.3	53.9	43.2	96.6	36.8
	79.8	52.0	16.1	19.7	112.0	55.4	58.4	55.2	45.8	87.2	37.7
	83.7	56.1	16.5	21.1	113.4	62.3	68.1	56.8	46.8	92.1	39.3
AQUILA2	92.7	54.8	17.8	20.2	113.4	61.9	64.3	54.5	46.3	85.7	35.9
	91.0	57.1	18.7	22.7	121.9	60.9	69.7	69.2	47.6	93.0	40.1
	88.2	56.1	18.7	21.3	122.2	63.2	73.5	55.3	44.6	92.2	37.4
	94.4	61.4	19.8	21.6	121.4	61.3	69.7	57.6	47.5	92.6	41.6
HALIAEE	82.3	50.1	16.7	19.0	126.8	57.5	56.2	55.4	48.1	100.4	40.7

APPENDIX 12.5 continued

C Coracoid, furcula, and scapula

	Coracoid			Furcula		Scapula					
Genus	L	Wf	Ws	Wst	W	Hdv	Hap	L	Lh	Wn	Wb
HARPIA	69.3	22.2	11.2	25.0	59.6	53.0	29.7	94.4	21.4	7.9	13.5
	82.9	25.6	13.7	30.3	77.0	66.4	37.1	111.7	27.0	9.6	17.3
	72.0	22.3	11.2	26.1	64.9	53.6	-	97.9	22.7	8.7	13.8
	78.4	23.5	12.4	28.7	80.5	62.8	30.0	106.2	26.6	9.2	18.1
PITHECOP	73.4	19.8	13.1	28.4	76.2	56.3	31.7	100.5	24.5	9.8	14.1
	79.2	23.9	13.1	31.2	79.8	61.2	32.0	109.0	27.7	10.2	14.5
POLEMAET	76.9	23.7	13.3	31.9	71.3	56.9	38.4	100.8	25.9	9.0	15.1
	81.7	23.7	13.6	33.5	-	56.6	44.1	105.3	27.0	9.1	14.2
	75.2	23.7	13.3	29.2	78.3	58.7	34.3	97.5	23.5	8.9	14.9
	-	-	-	-	-	-	-	-	-	-	-
	78.2	24.4	19.3	31.4	76.5	61.8	42.2	103.7	25.3	10.0	15.8
STEPHANO	71.2	20.9	11.8	25.9	71.3	51.2	29.0	97.2	22.1	8.2	13.7
	71.6	21.6	12.5	26.8	71.0	52.9	28.8	97.0	23.5	8.4	15.3
SPIZAETU	48.9	13.3	7.1	19.1	40.6	35.4	19.1	66.9	14.4	6.1	9.9
	44.9	13.5	6.5	14.8	35.4	35.3	18.9	60.3	14.1	5.1	8.5
MORPHNUS	50.9	15.0	7.2	17.3	50.3	37.8	20.1	73.4	15.4	5.8	9.5
LOPHOAET	50.2	15.0	6.9	18.7	50.9	34.4	20.8	65.4	15.2	5.2	9.8
	49.7	13.7	7.7	19.5	50.2	38.5	19.8	66.2	15.3	5.8	9.9
	49.9	14.5	6.8	19.2	47.1	37.5	17.3	66.6	14.8	5.0	9.9
	49.2	13.9	7.1	18.9	47.3	34.2	21.2	64.6	14.6	5.6	9.2
AQUILA1	73.7	22.0	12.9	29.3	74.3	54.5	35.9	91.9	23.7	9.2	13.5
	72.3	23.2	11.8	27.5	72.2	56.2	32.4	94.1	25.0	8.7	13.7
	67.1	21.0	12.0	27.6	77.4	50.6	25.7	88.2	22.8	8.3	12.0
	71.8	22.3	13.3	28.9	77.9	55.8	31.2	94.4	23.9	9.7	14.8
AQUILA2	71.1	21.0	10.7	26.6	67.2	56.6	32.3	89.8	23.8	8.1	11.6
	76.0	23.5	13.8	30.0	79.2	58.0	32.5	96.2	25.1	8.3	12.9
	75.7	21.9	11.9	27.9	70.3	55.2	30.1	91.3	23.3	8.0	12.4
	76.2	23.1	13.1	30.8	80.5	54.3	26.7	97.8	24.3	9.8	11.8
HALIAEE	77.9	23.3	12.6	28.9	77.4	58.9	31.7	93.1	24.8	7.9	15.1

D Humerus, ulna, carpometacarpus, phalanx 1 major digit

	Humerus				Ulna				Cpm			Phal. I	
Genus	L	Wp	Wd	Sdc	L	Pdv	Pav	D	L	Wp	Wd	L2	W
HARPIA	164.0	34.8	30.8	12.9	187.5	20.9	14.8	14.3	87.4	23.9	16.3	31.4	12.6
	204.7	44.3	37.2	17.8	244.1	24.7	17.6	18.2	106.8	27.7	18.2	37.6	14.8
	173.3	37.3	32.5	13.7	200.7	21.5	14.5	15.7	90.4	23.9	15.6	29.4	13.1
	190.3	42.2	37.1	16.8	229.0	23.5	16.1	14.1	100.0	27.3	18.6	36.6	14.2
PITHECOP	185.9	37.2	33.1	15.0	213.3	21.1	15.9	14.5	92.8	24.9	15.4	35.9	13.7
	193.6	39.9	36.0	15.3	219.6	23.8	16.5	14.6	95.8	25.3	18.2	36.8	14.7
POLEMAET	203.7	39.8	33.6	14.0	251.9	23.1	16.4	14.6	110.7	26.0	18.6	42.9	16.1
	208.7	42.4	35.0	14.7	251.2	24.6	17.4	14.5	116.6	27.5	20.6	44.1	15.4
	191.7	37.3	33.9	15.2	232.9	22.8	17.3	14.6	108.1	26.1	17.7	41.0	15.0
	211.1	40.5	34.8	15.7	258.2	24.8	16.7	16.1	116.9	27.4	20.3	43.5	15.8
STEPHANO	166.9	36.2	31.8	14.3	201.6	21.1	13.7	14.5	86.9	22.4	15.0	29.2	12.8
	167.8	37.5	32.7	14.6	198.4	22.4	15.4	13.6	-	-	-	-	-
SPIZAETU	111.6	23.5	21.3	9.3	132.5	14.5	10.3	9.7	-	-	-	22.7	9.3
	100.8	22.0	18.6	8.4	120.6	12.7	8.9	8.1	54.1	14.8	10.3	20.8	8.2
MORPHNUS	130.1	24.8	22.4	9.4	149.0	15.6	10.7	10.3	65.3	16.5	-	24.1	10.1
LOPHOAET	121.2	22.9	19.9	8.6	137.2	13.9	10.1	9.7	62.2	16.5	11.1	24.3	9.7
	121.9	23.2	19.9	9.3	137.7	14.0	10.2	9.3	64.7	15.9	11.5	25.5	9.8
	117.6	23.7	19.3	9.2	133.5	13.4	10.2	10.1	62.0	15.8	12.7	24.5	9.9
AQUILA1	180.1	36.8	31.3	13.8	210.8	21.5	15.8	13.4	101.7	24.6	15.9	36.3	15.5
	177.9	40.8	32.9	13.7	212.0	23.1	16.2	13.9	100.5	26.1	18.6	38.8	15.6
	164.9	37.3	30.0	12.8	191.3	20.3	14.9	13.1	91.7	23.1	16.8	33.2	13.4
	175.5	38.4	32.1	14.2	200.7	21.6	16.5	13.7	97.2	25.3	17.2	36.2	15.2
AQUILA2	188.6	36.7	31.0	13.1	228.3	21.8	15.5	15.5	104.7	25.8	18.4	40.1	15.3
	192.8	39.3	32.7	14.5	230.3	22.9	16.5	15.3	107.1	26.4	19.3	42.6	16.5
	190.6	40.9	32.2	14.1	225.2	22.1	16.3	14.6	101.5	25.4	18.1	40.6	16.5
	192.9	40.0	32.4	13.5	228.0	22.7	-	14.5	109.1	-	19.6	42.7	16.8
HALIAEE	190.1	37.9	32.5	13.4	227.9	22.2	15.3	13.9	107.1	24.8	17.4	44.7	13.9

APPENDIX 12.5 continued

E Pelvis, pygostyle, femur

	Pelvis						Pygo	Femur				
Genus	L	Wp	Ww	Wi	Wpi	Wi	L	L	Wp	Wd	Ssag	Smed
HARPIA	119.7	40.0	23.1	32.9	54.9	38.4	38.2	112.1	27.6	29.7	12.5	12.8
	147.4	44.6	26.5	34.2	59.2	55.0	47.3	129.7	33.9	37.3	15.2	15.7
	125.1	44.0	26.1	31.2	56.9	46.1	-	119.8	27.9	30.1	12.9	13.2
	140.8	44.8	28.0	31.7	54.0	46.4	38.9	120.4	30.8	35.0	15.4	15.3
PITHECOP	134.2	41.6	23.6	33.5	57.4	50.3	41.0	123.0	27.9	31.2	13.1	13.7
	140.9	43.3	24.4	34.1	60.7	54.8	43.1	126.3	32.1	34.6	14.6	15.7
POLEMAET	118.6	48.0	24.9	33.2	51.6	46.5	40.1	125.3	27.2	28.9	12.6	12.2
	132.6	50.0	25.0	36.2	60.1	54.8	43.8	130.8	30.2	31.9	13.9	14.2
	121.3	48.7	26.8	35.7	56.9	47.8	41.3	121.8	26.9	28.1	13.2	13.7
	-	-	-	-	-	-	-	-	-	-	-	-
	127.8	46.8	27.9	39.5	59.8	53.0	42.8	130.6	27.3	30.8	14.8	14.7
STEPHANO	125.6	38.5	23.1	34.2	60.1	46.3	42.2	113.1	26.7	28.8	13.3	13.2
	122.4	37.4	23.1	35.3	59.1	44.4	-	113.9	28.2	30.1	13.7	14.2
SPIZAETU	78.2	31.1	18.1	25.4	39.1	35.8	-	87.2	18.0	19.9	9.0	8.4
	73.0	26.7	16.0	23.9	34.4	28.2	25.7	79.9	16.8	17.8	7.9	7.7
MORPHNUS	88.9	34.5	15.7	24.7	43.4	33.0	31.7	92.3	17.9	19.8	9.2	9.6
LOPHOAET	81.9	32.6	19.4	28.5	43.9	29.3	22.7	90.1	17.3	19.5	8.2	8.3
	80.8	32.6	19.1	27.7	39.7	30.4	26.1	88.6	17.5	19.4	8.8	9.0
	79.7	31.9	19.4	29.9	42.5	29.4	-	88.1	17.1	19.9	8.0	8.1
	-	-	-	-	-	-	-	-	-	-	-	-
AQUILA1	118.8	49.3	29.8	38.9	58.7	46.7	37.4	124.9	25.4	27.0	12.1	11.9
	121.3	47.2	28.6	40.6	58.0	40.3	40.3	123.9	27.2	29.2	11.7	11.9
	111.9	39.4	28.6	39.3	58.0	46.0	-	105.6	24.5	27.6	10.7	11.2
	119.5	47.3	31.4	38.7	56.7	46.9	39.4	121.5	27.0	29.1	12.3	12.1
AQUILA2	119.8	46.4	26.9	26.9	57.6	44.8	36.5	118.2	26.6	27.9	12.3	12.2
	127.2	51.1	31.2	39.4	60.7	48.1	41.1	116.7	26.8	28.9	12.6	13.1
	125.5	49.8	28.5	34.0	-	-	43.0	120.0	27.3	30.0	12.6	12.3
	123.4	50.8	29.6	36.8	62.5	53.1	47.1	120.1	27.6	29.9	12.8	12.0
HALIAEE	119.4	47.2	26.3	36.0	52.8	-	37.5	104.3	24.1	25.5	11.3	11.7
HARP33	183.8	58.4	39.8	58.5	82.0	59.4	-	-	-	-	-	-

F Tibiotarsus, tarsometatarsus

	Tibiotarsus						Tarsometatarsus							
Genus	L	Wp	Wd	Ssag	Smed	Fib	L	Wp	Wd	Dic	Dec	Din	Dd	Met
HARPIA	155.5	29.2	26.0	10.0	11.6	61.3	101.3	26.7	27.1	18.6	16.3	7.4	18.2	61.6
	192.3	36.6	29.8	11.7	13.2	70.6	117.8	30.6	33.0	23.3	18.6	9.0	20.8	67.1
	163.3	29.8	26.1	10.2	11.8	65.3	105.0	26.2	28.9	19.0	16.6	7.7	17.6	64.5
PITHECOP	196.2	29.5	23.2	10.3	11.6	74.4	120.7	24.3	26.8	18.7	15.1	8.8	15.1	82.8
	199.1	33.6	24.8	11.1	12.9	76.4	118.0	26.3	29.3	20.2	16.3	9.0	16.1	80.8
POLEMAET	186.0	27.5	22.2	9.2	11.7	74.3	119.5	23.8	27.6	19.0	16.3	8.5	18.5	82.3
	181.6	30.3	24.4	9.6	11.9	69.2	122.4	25.1	27.4	19.2	16.3	9.5	18.8	83.1
	176.7	27.6	21.2	9.0	12.2	70.4	121.8	22.4	25.3	17.9	14.9	8.7	16.3	85.9
	-	-	-	-	-	-	124.2	25.3	28.1	19.5	16.2	9.3	17.4	84.7
	186.3	29.2	22.9	10.0	12.9	70.6	124.9	24.6	28.5	19.4	16.1	8.7	18.5	88.3
STEPHANO	160.4	27.9	24.0	9.8	11.4	66.5	100.5	24.0	26.2	18.0	15.5	6.8	16.2	65.8
	157.9	30.8	25.1	10.4	12.3	62.1	100.8	26.2	28.3	19.4	16.7	7.3	18.5	62.0
SPIZAETU	126.9	19.0	15.6	6.5	7.9	45.0	89.9	15.9	18.4	13.5	10.8	6.3	10.8	64.3
	114.1	16.8	13.3	5.6	6.8	40.8	82.2	14.1	15.8	11.2	9.3	5.3	9.8	59.4
MORPHNUS	145.6	19.5	15.2	6.5	7.6	53.1	102.2	15.8	17.6	11.9	9.9	5.1	9.2	76.6
LOPHOAET	129.3	18.4	14.6	6.6	7.5	47.8	96.8	15.0	17.6	12.0	10.3	6.1	10.7	74.8
	-	18.5	14.7	-	-	-	96.2	15.0	18.1	11.8	10.0	6.1	11.1	72.3
	125.4	17.4	14.1	6.1	7.2	46.9	94.2	14.6	15.5	12.0	10.4	6.4	-	71.8
AQUILA1	167.3	26.8	20.2	8.2	10.5	63.7	105.3	21.3	24.3	16.7	14.2	8.8	15.0	74.0
	169.5	28.4	21.4	8.0	10.6	66.0	104.3	22.9	25.3	17.6	14.9	8.2	16.4	72.1
	152.9	24.9	19.7	8.8	10.4	60.3	99.8	20.0	21.7	15.3	12.5	7.0	14.1	70.2
	159.7	26.9	20.9	8.5	11.0	60.5	97.6	21.6	23.1	17.2	12.8	8.0	14.9	66.7
AQUILA2	168.8	27.0	20.1	8.3	10.1	65.0	109.0	21.0	25.4	17.8	14.1	8.3	15.0	77.8
	169.0	28.3	21.1	9.2	11.1	68.3	110.3	21.4	25.9	17.7	14.2	9.8	15.6	78.5
	171.6	28.3	21.4	8.9	10.5	66.4	107.1	22.6	25.4	18.1	14.6	8.4	15.9	72.8
	171.8	27.2	21.6	9.7	10.4	67.6	112.0	22.0	26.0	17.7	14.5	9.2	15.0	74.9
HALIAEET	153.7	24.7	18.7	8.0	9.9	54.4	101.8	19.3	23.9	16.1	12.0	8.7	12.8	68.2

APPENDIX 12.5 continued

G Ungual phalanx, pedal digit I

	Ungual phalanx			
Genus	L	Dp	Dcon	Dcl
HARPIA	54.4	24.4	16.8	11.6
	61.1	29.8	21.8	12.9
	55.9	25.2	16.9	11.3
	62.2	28.6	20.7	11.7
PITHECOP	47.9	21.0	14.1	7.9
	49.6	23.1	15.0	10.4
POLEMAET	50.0	23.1	15.3	9.3
	49.3	24.3	16.3	9.0
	48.5	22.8	15.0	9.0
	49.0	23.7	15.7	9.6
	50.0	23.7	15.1	9.2
STEPHANO	47.4	23.4	15.7	11.5
	-	-	-	-
SPIZAETU	33.8	15.8	10.6	6.7
	31.5	13.5	8.8	5.4
MORPHNUS	28.6	-	8.7	5.9
LOPHOAET	33.3	13.0	8.9	5.0
	32.9	11.6	8.0	5.6
	26.3	12.7	9.0	4.6
	-	-	-	-
AQUILA1	43.7	17.9	12.2	8.4
	45.5	19.5	13.3	9.0
	38.0	17.6	11.3	7.2
	41.2	18.6	12.6	7.7
AQUILA2	36.5	17.9	11.7	7.2
	40.2	18.9	12.7	8.3
	37.4	18.3	11.8	8.1
	40.8	19.2	14.5	8.3
HALIAEET	36.2	16.9	10.8	7.8

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